University of Alberta

Wind changes crown and stem form of large lodgepole pine

by

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Dedication

To my parents, my wife Ling Wang and my son Larry Meng

Abstract

Wind-induced crown collisions were hypothesized as the cause of crown shyness. To prevent crowns from colliding in wind, groups of 15 m tall lodgepole pine (*Pinus contorta* Var. *latifolia* Engelm.) trees were tethered in a web pattern in four stands in Alberta, Canada. To assess changes in crown closure, canopy photographs were taken in each plot in 1998 and 2004. Six years later, webbed trees had increased crown cover and leaf area. Crowns of webbed trees were more symmetrical and porous than crowns of control trees. Those results supported the hypotheses that crown collisions play a crucial role in the formation of crown shyness that leads to the reduced leaf area and productivity of older stands.

I also tested the hypothesis that bending moment produced along the bole when wind acts on the crown, limits height growth, increases radial growth, and changes wood properties. In the same stands as above, I found that reducing bending moment resulted in increased height growth relative to pretreatment (40%), comparing to a nearly 20% drop for control trees. The quantification of the radial growth to bending moment has shown that radial growth and wood property are closely related to the bending moment applied along the bole. The ratio of bending stresses at the height of 10m to 1.3m was close to 1 for control trees, suggesting a uniform stress distributed along the bole.

As bending moment strongly affects the C partitioned on radial growth relative to height growth, I further hypothesized that the scaling exponent of diameter-height of trees is governed by the bending moment. Using data from repeatedly measured lodgepole pine trees, I found that basal area increment (BAI) relative to height growth increased with the bending moment; the scaling exponent was strongly correlated with the bending moment.

The strong relationship between bending moment and stem size led me to propose new

models for prediction of BAI, crown volume and crown radius of lodgepole pine. New models explained 74, 69 and 61 percent of total variation of BAI, crown volume, and crown radius respectively using data sets collected from permanent sample plots.

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Chapter 1: Introduction

In the natural world, wind is an environmental parameter as ubiquitous and fluctuating as light or other factors, but it has received comparatively little attention as a factor affecting plant growth (Ennos 1997; Berthier and Stokes 2005). Being a major force profoundly shaping the evolutionary history of terrestrial plants (Niklas 1998), wind affects plant growth in various ways: morphologically, wind-induced crown collisions cause direct breakage of needles, twigs and branches of trees (Putz et al. 1984; Long and Smith 1992; Rudnicki et al. 2001; 2003), which was hypothesized to be the key mechanism that drives the formation of crown shyness, i.e., the empty spaces that surround the crowns of trees that not attributable to missing trees. Touching and rubbing of branches caused by tree sway has been shown to produce thigmomorphogenetic effects: increase in radial growth and reduce in cell elongation (Telewski and Jaffe 1981; 1986). More importantly, the bending moment produced when wind force acts on crowns has been demonstrated to have profound impacts on carbon partitioned between the above ground and below ground biomass (Stokes et al. 1995; Stokes et al. 1997; Urban et al. 1994; Henry and Thomas 2002), between leaf area growth and stem growth (Telewski and Pruyn 1998), and between height growth and radial growth (Larson 1965; Telewski and Jaffe 1986; Valinger 1992; Jacobs 1954; Burton and Smith 1972; Telewski and Pruyn 1998). Plants subjected to steady winds usually have a stunted appearance, apparently growing in a way to efficiently cope with the wind force (Ennos 1997; Metzger 1893; Niklas 1998). Physiologically, wind-induced bending moment has been reported to affect the hydraulic conductance of the stem by anatomically changing the property of sapwood to conduct water (Liu et al. 2003; Larson 1965; Dean 1991). Wind also affects the air flow around the boundary layer surrounding the foliage (Oke 1987; Telewski 1995), consequently having an impact on water transpiration, vapour pressure deficit and processes of photosynthesis.

Crown collisions and crown shyness

As an ecological factor, wind affects plant growth not only in extreme events such as storms or hurricanes but also in chronic moderate to high speed winds (Ennos 1997). The crown collisions due to tree sway from moderate wind events cause the breakage of twigs and branches, loss of foliage, inhibition of shoot extension (Rees and Grace 1980; Robertson 1987; Grier 1988; Long and Smith 1992; Putz et al. 1984; Telewski and Jaffe 1986), and are implicated in the formation of crown shyness, which is thought to lead to the decline in leaf area and productivity

when stand ages (Ryan et al. 1997; Long and Smith 1992; Rudnicki et al. 2001; 2003). Crown shyness develops in older stands and its onset is approximately at the time of peak leaf area and culmination of periodic annual increment (Smith and Long 2001). It has long been assumed that crown shyness is attributable to poor light conditions between crowns (Chen et al. 1996; Mäkelä 1997), which eventually limits the lateral development of branches. However, increasing evidences show that crown collisions play a crucial role in driving the formation of crown shyness (Long and Smith 1992; Rudnicki et al. 2001; 2003), but this has never been experimentally tested.

Bending moment and upper limit to height growth

When a wind force acts on the crown, it produces an increasing bending moment toward the base of the stem. It has been assumed that selection pressure has resulted in tree stem biomechanics that could effectively resist this bending moment, to prevent failure of stems due to wind (Niklas 1998; Ennos 1997; Jaffe 1973; King 1986; Vogel 1989; Mattheck 1991). The basal diameter required for stability of the tree scales exponentially with height (McMahon 1973; King 1981; King 2005). As a tree increases in height, so does the bending moment. Hence, to maintain the mechanical stability of tall trees, any further increase in height would require trees to invest carbon (C) exponentially into radial growth of the stem. As there is also reduced leaf area and C fixation when trees grow taller and older (Ryan et al. 1997), I therefore proposed that increasing bending moment will drive tall trees to assign increasingly more of the available C to radial growth relative to height growth. These mechanical constraints will eventually result in trees approaching an upper limit to their height. It has also been hypothesized that hydraulic limitation due to increased resistance as trees grow taller will constrain the water movement and drive a tree to approach its upper limit (Ryan and Yoder 1997; Niklas and Spatz 2004; Koch et al. 2004). However, recent studies testing the hydraulic limitation hypothesis found that hydraulic limitation in large trees is common, but not universal (Ryan et al. 2006). Therefore, there should be other factors limiting height growth in trees (Pennisi 2005; Ryan et al. 2006).

Bending moment and stem form

It has long been noticed that wind force affects the C allocated for height growth relative to radial growth (Knight 1803; Jocabs 1954; Larson 1965; Burton and Smith 1972; Valinger 1992). Regarding the impact of bending moment due to wind force on radial growth along the bole, it has been proposed that a tree stem grows in such a way to counter the bending moment that it tends to equalize the bending stress applied at the outer surface of the bole (Metzger 1893). The

basic hypothesis is that, to maintain mechanical stability, stem growth at any given height of a tree tends to be related to the amount of bending moment applied there. There were some studies conducted to test this hypothesis by comparing the stem profile to the static bending stress (Milne and Blackburn 1989; West et al. 1989; Morgan and Cannell 1994), or testing a theoretical relationship between diameter and bending moment (Dean et al. 2002; Dean 2004). However, the study designed to quantify the bending moment along the bole and the corresponding radial growth and wood property (latewood: earlywood) has not been found.

As wind force affects the radial and height growth, it would also affect the allometric relationship of diameter to height. There were attempts to describe this allometric relationship using principles of mechanical design. However, the past three models proposed based on the mechanical theory all claimed a constant scaling exponent (β) between DBH and height (McMahon 1973; Rich 1986; Rich et al. 1986; McMahon and Kronauer 1976), which deflects from the real trend that β increases with age (size) of tree (Niklas 1995; King 1996). One important factor neglected in the past models is the bending moment, which has been shown to have a big impact on radial growth relative to height growth (Larson 1965; Valinger 1992). Given its potential role on stem growth, I proposed that increasing bending moment drives the increase of β when trees grow taller and bending moment governs the allometric scaling exponent of DBH to height of trees.

Application of the bending moment-stem size relationship

Resisting the bending moment produced from the wind and maintaining the stability of the tree are critical for tree's survival (Schniewind; 1962). To counter the bending moment, trees have shown great flexibility to reallocate their carbohydrate between aboveground and belowground structures (Stokes et al. 1997; Urban et al. 1994; Henry and Thomas 2002), and between radial growth and height growth (Telewski and Jaffe 1981; Telewski and Jaffe 1986; Telewski and Pruyn 1998). The amount of C allocated for basal area growth relative to height growth of a tree is closely related to the bending moment the tree is subjected to. Given that the total carbon pool a tree can produce is a function of its crown dimensions, I proposed that bending moment, estimated as the product of crown frontal area, wind speed and leverage, can be served as a predictor of basal area increment. As a tree has to keep its balance among crown size, bending moment and stem size, to maintain the stability, I also expected that crown volume can be estimated from the stem size and leverage. Dean (2004) developed a useful model to describe the theoretical relationship between basal area increment and changes of bending moment over a growth period, based upon the uniform stress theory. In Dean's model, however, the leaf areas at

both the beginning and end of a growth interval are required for calculation of bending moment, which limits its application for prediction of growth. In addition, the effects of social position and stem density on wind pressure of each individual tree subjected were neglected in Dean's model.

Summary of research opportunities

In spite of the increasing evidences show that crown shyness might be linked directly to mechanical abrasion induced by tree sway, the studies designed to test this hypothesis are still missing. The light limitation hypothesis has apparently ignored the importance of wind force on crown development through its induction of collisions and touching of a tree's branches with its neighbours branches. By preventing crown collisions by tethering together groups of maturing lodgepole pine trees, it would be possible to test the hypothesis that crown abrasions and collisions in wind play a crucial role in driving the formation of crown shyness, and in triggering the decline in stand productivity because of reduction in leaf area. From examining the height growth of large trees following the treatment of reduction in bending moment, it will enable me to test the hypothesis that increased mechanical constraints when trees grow taller, slows its growth in height and drives it to approach the upper height limit. The further examination of wood properties and quantification of bending moment and radial growth can give us a better understanding of the response of tree stems to mechanical stimuli and test the uniform stress hypothesis. Understanding of the roles of crown collisions on crown shyness, the bending moment on stem form and wood property can aid foresters to improve the stand productivity and wood quality from manipulation of stand density or selection of population of trees that could efficiently resist wind sway. Closely examining the relationship between bending moment and radial growth can also bring the opportunities to build models for prediction of basal area growth and crown volume based upon principles of mechanical design. The following are some important ideas that need further study to advance the understanding of the wind force on crown shyness, ultimate height growth, and stem form.

1. Directly test the potential role of crown collisions on crown cover and leaf area of trees that experience crown shyness.
2. Test the effect of mechanical constraints on ultimate height growth by reducing the bending moment induced from wind force on large trees.
3. Quantify the relationship between bending moment and radial growth and wood property (ratio of latewood to earlywood) along the bole, to test the uniform stress theory.
4. Re-examine the allometric scaling exponent of diameter to height of trees based on

the principles of mechanical design, with the consideration of the role of bending moment.

5. Model basal area increment by using the strong relationship between bending moment and radial growth.

6. Model crown volume based upon uniform stress theory.

Research objectives

I examined the impacts of wind induced tree sway on crown shyness, and the impacts of the bending moment on ultimate height growth and stem form of maturing, large lodgepole pine. I also developed models for prediction of basal area growth and crown volume of lodgepole pine, based upon the strong relationship between bending moment and radial growth, and uniform stress theory.

In Chapter 2, I investigated whether preventing crowns from colliding during wind would affect the amount of crown shyness, and consequently, the leaf area of a forest stand. To minimize the effects of wind sway on crown shyness, groups of trees at the height of 15m were tethered together at the height of 10m (base of live crown) in a web pattern from four stands across Alberta, Canada. I hypothesized that such prevention of crown collisions would decrease branch breakage and increase lateral growth, resulting in less crown shyness. I also hypothesized that leaf area of trees after receiving webbing treatment will be greater than that of control trees after several growing seasons.

Chapter 3 enabled me to test my hypothesis that reducing mechanical constraints via bending moment will increase the height growth of large lodgepole pine that were declining in height growth. Trees with a height of 15m were tethered at the height of base live crown to counter the wind force, therefore reducing the bending moment applied at the bole. I hypothesized that reducing bending moment will increase height growth. In addition, I also examined the impacts of bending moment on radial growth and wood property (ratio of latewood to earlywood) by quantifying the relationship between bending moment and stem growth. I hypothesized that reducing bending moment will increase the radial growth and reduce the proportion of latewood to earlywood.

In Chapter 4 I examined the role of bending moment on the allometric scaling exponent of diameter-height of trees. I hypothesized that the increase of bending moment results in increased C allocated for basal area increment relative to height growth. This increased partition of C on radial growth relative to height growth will affect the scaling exponent of diameter to height.

In Chapter 5, I proposed a new model for prediction of basal area increment of lodgepole

pine based upon the strong relationship between bending moment and radial growth. In addition to the bending moment (product of crown frontal area and leverage), other predictor variables entered in the model included site index, relative depth to the zero plane displacement and stand relative density which were taken as a surrogate of wind speed.

In Chapter 6 I developed a new model to predict crown volume of lodgepole, based upon the uniform stress theory. Independent variables included DBH, leverage, mean wind speed of the site and relative depth to the zero plane displacement and stand relative density, a surrogate of wind exposure for each individual tree.

In chapter 7, I drew the conclusions for this thesis and discussed some research opportunities that could be carried out in the future for further understanding of the effects of wind, individually or interactively with other ecological factors, on growth and morphology of trees.

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Chapter 2: Reducing crown collisions increases crown cover and leaf area of maturing lodgepole pine[1]

Introduction

Reduced leaf area has been ascribed to be a key factor triggering the initiation of decline in productivity when forest stands age (Ryan et al. 1997). This reduction in leaf area has been considered to be related to reduced nutrient availability in older stands (Gower et al. 1992; Gower et al. 1995), or loss of leaf area and canopy closure because of crown shyness, i.e, the open area surrounding the crowns of trees in fully-stocked stands that is not attributable to tree mortality (Putz et al. 1984; Oliver and Larson 1996). Crown shyness develops in older stands and its onset is approximately at the time of peak leaf area and culmination of periodic annual increment (Smith and Long 2001). It has long been assumed that crown shyness is attributable to poor light conditions between crowns (Chen et al. 1996; Mäkelä 1997), which eventually limits the lateral development of branches. However, recent studies show that direct abrasion and growth inhibition caused by wind induced crown collisions are strongly implicated in the development of the peripheral spaces surrounding tree crowns (Long and Smith 1992; Rudnicki et al. 2001, 2003). As trees become taller, a tree with a slender stem (high height/diameter at breast height), swaying in the wind hits adjoining crowns with increasing force, pruning the twigs and buds, thereby resulting in a narrow crown form with wide spaces between crowns (Long and Smith 1992). More recently, the sway of a group of trees was monitored using biaxial clinometers by Rudnicki et al. (2003); they found that a stand with slender trees had lower crown cover, greater sway displacement, faster sway speeds, and a greater depth of collision with neighbouring trees compared to a stand with stout trees. This suggests that collisions with neighbours caused by wind played a crucial role in limiting crown development. The narrow crown form typical of lodgepole pine trees (*Pinus contorta* Dougl. Ex Loud. Var. *latifolia* Engelm) in stands at peak leaf area might also be as a result of thigmomorphogenesis; a growth response elicited by branches contacting each other in wind resulting in an increase in radial enlargement and a decrease in branch elongation (Larson 1965; Telewski and Jaffe 1981; Telewski and Jaffe 1986). Regardless of whether crown shyness is a result of abrasion or thigmomorphogenesis, it has been hypothesized that declining leaf area in older stands is related to contact and collisions of crowns during wind (Grier 1988; Foster and Boose 1992; Ryan et al. 1997), but this has never been experimentally tested.

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The objectives of this study were to investigate if preventing crowns from colliding during wind would affect the amount of crown shyness, and consequently, the leaf area of a forest stand. To minimize the effects of wind sway on crown shyness, a group of lodgepole pine trees were tethered together into a web like structure to prevent crowns from colliding during wind events. I sought to test the hypotheses (1) that prevention of crown collisions as a result of webbing would decrease branch breakage and increase lateral growth resulting in less crown shyness; and (2) that leaf area of the webbed trees will be greater than that of control trees after several growing seasons.

Materials and Methods

I studied paired plots in four fire-origin, naturally regenerated, even-aged pure lodgepole stands across the foothills of Alberta: the Two Creeks site (TC) (54°20′N, 116°23′W) located 50 km west of Whitecourt, the Bighorn site (BI) (51°51′N, 115°22′W) located 50km west of Sundre, the Redrock site (RE) (54°32′N, 119°07′W) located 50 km south of Grande Prairie, and the Amundson site (AM) (54°33′N, 118°00′W) located 75 km south east of Grande Prairie. The BI site was later excluded from the analysis as some trees within the plot were found broken by wind, at the point of webbing. Those stands were 50 to 55 years old. All sites were either west facing or near the summit of local hills and all plots had no canopy gaps from death of dominant or co-dominant trees. At each site, two plots of similar landform, stem density and spatial distribution of trees were located within 25m of each other. Trees in the plots were about 15 m tall, slender (had high height/diameter ratio, Table 2-1) and exhibited crown shyness when the study was started. Except on the TC site, trees from each pair of plots were similar in size. Stand density index ranged from 1000 at the TC site, up to 1518 at the AM site. Ground cover was dominated by feather mosses across all sites.

At each site, one of the two plots was randomly selected for webbing treatment in the fall of 1998. To prevent trees from colliding in wind, 13-15 trees from treatment plots were tethered together using strong nylon rope in a web pattern at the height of 9-10 meters to minimize independent sway of the trees in wind. Boles were protected from rope abrasion by padded collars. This allowed the entire unit of webbed trees to sway in unison during wind and thus reduce their collisions. The edge of the web was attached to neighbouring trees at about 6 meters in height to dampen the sway of the entire web. Understory black spruce saplings (*Picea mariana* (Mill.)

B.S.P.) and/or shrubs were cleared from the plots to allow ladder access and to establish three permanent photograph points marked with a metal rod pounded into the ground. Clearing and photograph point establishment was also done in the control plots. In the fall of 1998, photographs were taken of the canopy with a SLR camera (Pentax MZ-M), using an 80mm lens. The camera was mounted on a tripod at a height of 1.7m and aimed vertically, oriented with a compass. After 6 growing seasons, in August, 2004, the canopy was re-photographed using the same protocol at the same photograph points to assess changes in crown closure.

Tree sampling

In fall of 2004, the base of all of the trees in the plots and those immediately outside of the plot were numbered and mapped, and height (ht), diameter at breast height (dbh) and height to live crown of all trees was recorded. All trees from both webbed and control plots were destructively harvested. After harvesting, the crown of each tree was equally divided into top, middle and bottom sections. Maximum crown width and crown width perpendicular to it were measured using a tape on each crown section. A sub-sample of fresh needles containing multiple cohorts from each crown section was sampled and stored on moistened plastic bags in a cooler and later refrigerated at 3°C until they were processed. All remaining live branches from each crown section were cut, bagged and transported to the lab for estimation of crown leaf area. To compare treatment effects on branch characteristics, three interior trees from both webbed and control plots were selected. The bole surface facing towards the inside of the triangle formed by the three trees was marked. Trees were cut and all the branches growing on the marked side of each stem from the top and middle sections of the crown were sampled. Branches were bagged, stored on ice and transported back to the lab for detailed measurements. Each of the sampled branches was surveyed for the presence or absence of polishing. Polishing was defined as a lack of needles and dark flaky outer bark with exposure of smooth, light brown inner bark on one or more sides of a branch.

The sub-samples of green needles from each crown section were scanned and one-sided, projected leaf area was measured using Sigma Scan-Pro image analysis software. All live branches were oven dried at 78 °C for one week. The needles were then separated from branches and oven dried at 78°C until a constant weight was reached. Specific leaf area (A_n, m^2g^{-1}) was determined for each crown section from the dry weight of the scanned sub-sample:

$A_n = A_p / w_n$

where A_p is the projected leaf area (m^2) and w_n is the dry weight of the needles (g). The leaf

area from each crown section was calculated by:

$A_l = A_n * w_B$

where A_l is the leaf area of the crown section and w_B is dry weight of the needles of that section.

Total leaf area of each tree was calculated by summing up leaf area from each crown section. Leaf area for individual branch samples was calculated as the product of branch dry needle weight multiplied by the specific leaf area of that crown section where the branch had grown. Crown volume was calculated assuming that crowns were elliptical in vertical profile. Crown radius was averaged from the two mid-crown width measures. Crown symmetry was calculated from these same two measures, by dividing crown width perpendicular to maximum crown width by maximum crown width.

Crown cover measurement

Negatives of canopy photos taken in 1998 and in 2004 were scanned using the same resolution and scaled to the same size (21×27 cm) on print-outs. On each print, three to four recognizable points of the canopy (such as point of connection of a rope to the bole, or the base of a branch) encompassing portions of the crowns of three or four trees were identified. The identical points were identified on the print of the paired canopy photo taken on the same photograph point six years later. A triangle or polygon was then constructed from those points to determine the area filled by crowns. First, a transparent paper was placed on top of the print. The tip of the longest branch for a crown within the polygon was identified and marked. This point served as the centre of a search circle with a radius of 1 cm (58cm at 10m height) to find the next longest branch tips in both directions. These points then served as centres for further searches to delineate the perimeter of the crown within the polygon. The same procedures were repeated on other crowns within the polygon. In cases where there were no other branch tips located within the search circle, the next closest tip was used. All marked tips from each crown were connected by drawing a straight line between each of the two closest tips, and the areas separating canopies and gaps were isolated (Figure 2-1). The transparent paper was then scanned and measured using Sigma Scan-Pro image analysis software to determine polygon and canopy areas. Crown cover was calculated by dividing canopy area by total polygon area.

Statistical analysis

This experiment was a randomized complete block design. Sites were treated as the random factor and the treatment was treated as the fixed factor. Treatment effects on crown cover changes,

leaf area and branch variables were analysed using Proc MIXED (SAS Institute, 9.1, Cary, N.C.). Because the variation of the variables caused by treatment was more of interest in this study, and no notable interaction was detected between sites and treatments, therefore, the table was presented by taking the average of each treatment across all sites. As only three of the four stands were sampled, the experiment had weak statistical power (the power was only 0.56 at α=0.1, δ=1.5, and σ=1.1. Where: α was significance level; δ was the difference of leaf area between treatment and control; σ was the variation of the samples). Therefore a critical α=0.1 was used for the experimental analysis.

Results

Six years after the webbing treatment, there was a significant increase in crown cover on webbed plots (P=0.06). Crown closure was 14.4 % greater than prior to treatment on the webbed plots, compared to a 2.1% increase for the control treatment (Table 2-2.).

Average leaf area (P=0.1587) and crown volume (P=0.2320) of webbed trees were 22.6%, 41.3% larger, respectively, than those of control trees for all of the sites, but these differences were not statistically significant (Table 2-2.). If only the three interior trees from which detailed branch data were collected were included in the analysis, however, leaf area per tree was significantly lower for the control than the webbed plots (P=0.041).

Webbing treatment resulted in a significant decrease (P=0.01) of crown density (leaf area/crown volume) relative to unwebbed controls (Table 2-2.). Crowns of webbed trees were more symmetrical in terms of crown shape at mid-crown section than control trees (P=0.06), which were clumped and asymmetrical (Table 2-2.). In fact, some branches from the control plots were so misshapen than they tended to grow in a steep upward curvature.

There were strong effects of tethering tree stems on the characteristics of the branches. For branches that pointed towards the interior of the three-tree triangles, mean branch length (P=0.017), leaf area per branch (P=0.027) and foliar density (leaf area per branch/mean branch length, m^2/cm) (P=0.021) of webbed trees were all significantly higher than those from control trees (Table 2-2.). Of the same unit length of branches, the leaf area of branches from control trees was over 30% lower than that of webbed trees. The number of branches that were polished due to chronic contact with neighbouring branches was significantly lower in webbed trees than

in control trees (P=0.031). On average, 38% of control tree branches were polished compared to 11% for webbed trees (Table 2-2.). Indeed, for control trees, the branches from the outer surface of the crown were often so polished that needle-bearing twigs were usually found only on the inner, protected side of the branch. Specific leaf area in webbed trees was lower than the control trees for all of the sites (Table 2-2.) but the differences were not significant (P=0.16).

Discussion

This study indicates that crown shyness and its accompanying loss of leaf area, in maturing stands are at least partially related to the collisions with neighbouring trees. This supports the hypotheses that wind and the resulting crown abrasion is a significant factor contributing to the decline in formation of crown shyness (Putz et al. 1984; Long and Smith 1992; Rudnicki et al. 2001). This is the first study to demonstrate that crown shyness can be reversed in maturing stands of trees if the crowns are prevented from colliding with each other during wind. Crowns in webbed stands covered an average of 14.4% more of the available canopy space in 2004 than they did in 1998. Because the light regime between crowns was not altered in this experiment, the notion that poor light quality inhibits lateral crown expansion is not supported by my results. I have also demonstrated that preventing collisions by webbing resulted in a significant increase in branch length, as well as the amount of foliage grown on those branches. This suggests that collisions as a result of tree sway are an important factor contributing to reduced leaf area and the associated decline in productivity when stands age, and trees reach a height where crowns sway at a sufficient velocity to produce damaging collisions (Rudnicki et al. 2003). The increase in branch length of webbed trees might also have been related to a decline in thigmomorphogenetic effect as contact between neighbouring branches was minimized. The increase in foliar density of individual branches, however, was more likely the result of prevention of direct abrasion and collisions with neighbouring branches as there was less polishing in webbed trees. The fact that three times as many of the branches in control trees were polished compared to webbed trees (Table 2-2.) suggests that collisions and resulting abrasion played a significant role in reducing the leaf area per branch. Indeed, the chronic abrasion in control plots apparently removed the lateral twigs in addition to the needles from the outer surface of mid-crown branches and polished the bark of these branches.

I noted there was a big variation of the changes in crown cover across all the control plots. The decrease in the crown cover in the control plot of RE site showed the expected trend in the

development of crown shyness after a stand has attained peak leaf area (Oliver and Larson 1996) (data not shown). However, a slight increase in crown cover was observed in control plots at TC and AM sites. This increase might be related to the reduced root competition associated with clearing the understory of the plots, because increased nutrients availability has been shown to increase branch growth (Amponsah, et al. 2005) and retention of lower branches (Amponsah et al. 2004). However, it is just as likely this increase in crown cover is related to the variation in intensity of wind storms at different locations over the six-year period. As abrasion events are mostly driven by periodic storms (Grier 1988) some of the stands may have had stronger abrasion events during the period of study, thus explaining the variation observed.

It is noteworthy that after six years of treatment, the crowns of webbed trees that were prevented from colliding were more symmetrical at the mid-crown than those of control trees (Table 2-2.). In contrast, control tree branches growing in proximity to near neighbours were typically curved upwards and shaped against the edge of the crown, contributing to crown asymmetry. It is not surprising that the mid-crown area showed the greatest evidence of polishing and curved branches as it is the widest part of the crown and thus most likely to collide with neighbouring trees during strong winds. My findings suggest that wind induced crown collisions plays an important role in shaping crowns. This adds new insights into factors that could exert potential influence in shaping tree crowns, in addition to the light hypothesis which suggests branches preferentially grow laterally solely to exploit light-rich spaces resulting in asymmetry of crown formation (Koike 1989; Sorrensen-Cothern et al. 1993; Chen et al. 1996; Cescatti 1997; Mäkelä 1997). Crown asymmetry induced by wind was also reported by Robertson (1987), who speculated that wind-induced tree sway was the primary factor underlying crown asymmetry and shyness in trees during the latter self-thinning stage of stand maturation.

While the webbing treatment significantly increased crown closure and leaf area per branch, there was no statistically significant increase in leaf area per tree, even though the mean leaf area for webbed trees was 22.6% larger than that of control trees (Table 2-2.). I speculate that the small sample size coupled with high variation among sites prevented me from detecting a statistically significant difference at the whole tree level. Further, as all of the trees in the plot were sampled, it is likely that the outer ring of webbed trees was still affected by abrasion from neighbours outside of the plot as crowns of similar sized trees swaying in wind were observed to be displaced 2.6 to 3.0 m in moderate wind events (Rudnicki et al. 2003). Indeed, if only the three interior trees were included in the analysis, leaf area per tree was significantly lower for the control than the

webbed plots (P=0.041).

This study also found preventing crown collisions resulted in a significant decline of leaf area density within crowns. I suggest that collisions with neighbours resulted in control trees having more compact and narrow crowns than the webbed trees because branches tended to grow upturned with twigs and needles facing inward. In comparison, after webbing the lateral branches of webbed trees expanded outward and therefore occupied more volume, but dispersed the foliage more widely forming a less dense crown. However, considering lodgepole pine is a slow growing species, I speculate more branches and leaf area would have filled in the crowns of these webbed trees if the experiment had been run longer.

In conclusion, my study demonstrates that preventing crowns of lodgepole pine from colliding during wind resulted in increased lateral growth of branches and more symmetrical crowns of individual trees, thereby increasing crown closure of stands. Six years after webbing, trees in webbed plots had individual branches with more leaf area and more foliage per unit branch length, as well as fewer branches with apparent polishing compared to trees in control plots. The branches of control trees were typically curved upward with twigs pointed inward, making the crowns more compact compared to the outwardly expanding crowns of trees from the webbed plots. Given that there was no change in the light regime between control and webbed plots, this is strong evidence against the hypothesis that crown shyness is caused by a lack of light.

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Table 2-1. Stand characteristics of control (c) and webbed (w) plots across sites in 1998, the year of plot establishment (Mean ± SE)

Plot	DBH (cm)	HT (m)	HT/DBH	Stand density (stems/ha)
TC_C	12.1±0.6	14.8±0.4	125.1±4.5	3200
TC_W	14.4±0.6	16.8±0.3	118.4±4.3	3200
AM_C	12.1±0.8	14.6±0.4	124.9±6.8	4000
AM_W	12.3±0.8	14.9±0.4	126.0±7.5	4400
RE_C	11.7±0.5	14.8±0.2	128.1±4.0	3800
RE_W	12.4±0.7	14.3±0.3	118.4±6.2	3600

Table 2-2. Means of response variables for lodgepole pine crowns for webbed and control plots, 6 years after webbing treatment (Mean ± SE; n=3).

Response variables	Webbed trees	Control trees	P value
Changes in crown cover (%)	14.4±2.9	2.1±6.2	0.06
Leaf area (m^2)	8.00±0.77	6.53±0.64	0.15
Crown volume (m^3)	4.39±0.82	3.09±0.41	0.23
Crown density (m^2/ m^3)†	1.92±0.13	2.36±0.15	0.01
Crown symmetry*	0.90±0.01	0.88±0.01	0.06
Branch length (cm)	71.1±2.1	59.3±1.0	0.02
Leaf area per branch (m^2)	0.15±0.01	0.09±0.01	0.03
Branch foliage density (m^2/cm) §	0.20±0.01	0.14±0.01	0.02
Branches polished (%)	11.3±5.9	38.4±2.9	0.03
Specific leaf area (cm^2/g)	33.2±1.4	34.3±0.6	0.16

† Crown density is the leaf area per crown volume

* Crown symmetry is the ratio of the smaller crown width to the maximum crown width, at the mid crown height.

§ Branch foliage density is the leaf area per branch length.

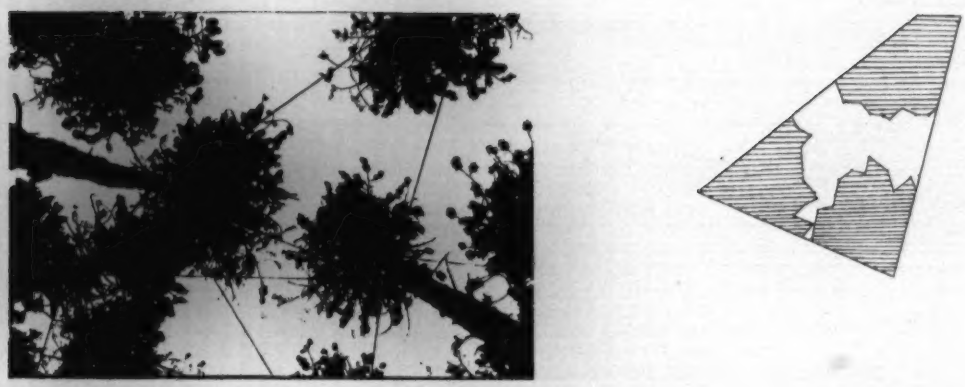

Figure 2-1. Left picture: Canopy photo taken at photograph from the webbed plot of TC site in 2004; right picture: polygon constructed based on left canopy photo; the dashed line inside the polygon was drawn by connecting selected branch tips; shadow area inside the polygon was crown cover area (see text).

Chapter 3: Reducing stem bending increases the height growth of tall pines[2]

Introduction

The reason why trees experience a gradual reduction in height growth as they become taller still remains unclear (Pennisi 2005). It has been hypothesized that hydraulic limitations in tall trees limits water movement (Ryan and Yoder 1997; Niklas and Spatz 2004), thereby limiting turgor pressure of leaf cells, stomatal conductance and CO_2 fixation (Koch et al. 2004). However, recent studies testing the hydraulic limitation hypothesis found that hydraulic limitation in large trees is common, but not universal (Ryan et al. 2006). Therefore, there should be other factors limiting height growth in trees (Pennisi 2005; Ryan et al. 2006). As trees are large, tall perennial plants, it has been proposed the selection pressure would result in stem biomechanics that could efficiently resist the bending moment applied to the tree from the forces of gravity and especially wind (Niklas 1998; Ennos 1997; Jaffe 1973; King 1986; Vogel 1989; Mattheck 1991). The basal diameter required for stability of the tree scales exponentially with height (McMahon 1973; King 1981; King 2005). As a tree increases in height, so does the bending moment. Hence, to maintain the mechanical stability of tall trees, any further increase in height would require trees to invest carbon (C) exponentially into radial growth of the stem. As there is also reduced leaf area and C fixation when trees grow taller and older (Ryan et al. 1997), it is therefore proposed that increasing bending moment will drive tall trees to assign increasingly more of the available C to radial growth relative to height growth; these mechanical constraints will eventually result in trees approaching an upper limit to their height. It has been reported that mechanical perturbation due to wind exposure, shaking, flexing or rubbing resulted in decrease in height growth of tree seedlings (Larson 1965; Telewski and Jaffe 1986a; Telewski and Pruyn 1998) and medium-sized trees (Valinger 1992), but it has not been experimentally test if reducing bending moment on mature, large trees which are declining in height growth would result in an increase in height growth.

It has been proposed that tree stems develop taper to counter the increasing bending moment toward the base of the tree when its crown is subjected to a wind load; bending stress applied at the outer surface of the stem tends to be uniformly distributed along the bole (Metzger 1893). The basic hypothesis is that, to maintain mechanical stability, stem growth at any given

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height of a tree tends to be related to the bending moment applied at that height (Milne and Blackburn 1989; West et al. 1989; Morgan and Cannell 1994; Dean and Long 1986; Dean 2004). However, in the past those testing the uniform stress theory concentrated either on the comparison of the static bending stress and stem profile (Milne and Blackburn 1989; West et al. 1989; Morgan and Cannell 1994), or testing a theoretical exponential relationship between diameter and bending moment (Dean et al. 2002). Some previous guying or staking studies (Jacobs 1954; Burton and Smith 1972; Valinger 1992) have reported stem growth after reducing tree sway, but the relationship of bending moment and stem diameter and height growth has never been quantified.

In addition to the potential impacts on C allocation along the bole, the mechanical perturbation has also been shown to affect the mechanical properties of the wood such as tracheid characteristics (Telewski 1989), modulus of elasticity (Telewski and Jaffe 1986a) and wood density (Telewski 1990), for efficiently resisting the mechanical forces and maintaining the mechanical stability of trees. It has been reported that following addition of sails or thinning treatments, the increased wind loads resulted in an increase in the ratio of high-strength latewood to earlywood (Larson 1965; Liu et al. 2003). However, there has been also a conflicting report that earlywood: latewood ratio is not affected by guying treatment (Burton and Smith 1972).

In this paper two hypotheses were tested: 1) that reducing bending moment of the bole will result in increased height growth; and 2) that diameter growth and wood properties of the stem are related to the bending moment applied to that section of the bole.

Materials and methods

Four fire-origin, naturally regenerated, pure, even-aged lodgepole stands across the foothills of Alberta were studied: the Two Creeks site (TC) (54°20′N, 116°23′W) located 50 km west of Whitecourt, the Bighorn site (BI) (51°51′N, 115°22′W) located 50km west of Sundre (which was later excluded from the analysis as some trees within the plot were found broken by wind at the point of tethering), the Redrock site (RE) (54°32′N, 119°07′W) located 50 km south of Grande Prairie, and the Amundson site (AM) (54°33′N, 118°00′W) located 75 km south east of Grande Prairie. Stands were 50-55 years old. Height growth of lodgepole in these areas usually peaks at about 15 years (6.3 m in height) and height growth rates decline thereafter (Huang et al. 2001). Lodgepole pine on these sites reach a maximum height of about 20 m at 100 years (Huang et al. 2001). All sites were either near the summit of local hills or west facing, thus exposed to

prevailing winds. Ground cover was dominated by feather mosses across the sites. At each site, two plots of similar landform, stem density and spatial distribution of trees were located within 25m of each other. Stand density ranges from 3200 stems per ha at the TC site to 4400 stems per ha at the AM site.

At each site, one of the plots was randomly selected for treatment. To control the bending moment produced by wind drag, in the fall of 1998, 13-15 trees from treatment plots were tethered together using a 12mm nylon rope in a web pattern at the height of 9-10 m, about 2/3 of the total tree height. Thus tethered trees were subjected to an external pulling force at the height of the tethering that countered the wind drag acting on the crowns (Figure 3-1). Boles were protected from rope abrasion by padded collars. The edge of the web was attached to neighboring trees at about 6 m in height. Understory black spruce (*Picea mariana* (Mill.) B.S.P.) saplings and/or tall shrubs were cleared from the plots to allow ladder access. Clearing was also done in the control plots to duplicate treatment conditions.

Tree measurements

In fall of 2004, the base of all of the trees in the plots and immediately outside of the plot were numbered, mapped and height, DBH and height to the base of the live crown were recorded. All trees from both tethered and control plots were destructively harvested. After harvesting, crown size, leaf area of each tree was carefully measured (see Meng et al. 2006). The height increment of the last six years was measured in the field by counting annual whorls. In cases where there was uncertainty of whorl counting, the stem was cut at the base of a questionable internode and rings were counted. Disks, 10-15 cm long at 1.3 m height were cut on each tree. In addition, 9 disks were cut at equidistant locations (1/10H) from the bottom to the top of each tree.

To measure the hydraulic characteristics, one meter stem section centered on the tethering height was cut from the tethered trees. The same section was also cut from control trees at the same relative height (about 10 m height). Right after the cutting, those 1m long sections were placed in double-wrapped polyethylene bags, stored in an insulated box covered with ice and later frozen at -15°C at the lab until further processed. A thin disk centered on tethering height was later cut from those 1m stem samples after completion of hydraulic measurement for both tethered trees and control trees. Therefore, a total of 11 thin disks were cut from each tree to measure the radial growth and wood property.

Stem disks measurements

As some of the boles of trees were deformed by western gall rust, only disks of the largest five healthy dominant/co-dominant trees were selected from each plot to examine the height and radial growth. These five trees were similar in size, spacing and slenderness coefficient (height/diameter at breast height) between tethered plot and control plot across sites (Table 3-1). Dominant trees were chosen because they occupied the upper layer of the canopy and were more exposed to wind. All disks of the five dominant trees from each plot were then dried and sanded. On each disk, the longest axis and the axis perpendicular to it were marked on the sanded side, and along each radius, the outer section (containing more then 12 rings) was wetted with glycerol and water and cut smooth using a razor blade. A stage micrometer (Velmex Inc., NY, USA) and dissecting scope was then used to measure the yearly ring width from 1993 to 2004 (to 0.001mm) along these four radii. The total length of each radius (inside bark) was measured to the nearest 0.001mm. For the disks cut at 1.3 m height and at the 10m height, the width of earlywood and latewood of each ring from year 1993 to 2004 was also measured on the four radii using the stage micrometer.

Past growth was reconstructed for each tree by doing stem analysis (annual ring analysis) from each of the stem sections; thus the height growth of the period 1993-1998, and stem volume growth five years before (1993 to 1997) and after the treatment (1999-2003) were estimated. Height-diameter increment ratio ($\Delta H / \Delta D$) was calculated by dividing the height increment by the mean diameter increment over each of the stem disks along the bole, for both the period 1993-1997 and period 1999-2003. Stem growth for 1998 and 2004 were excluded from radial growth analysis because the late wood ring for these two years were not fully developed when trees were tethered in the fall of 1998, or when they were harvested in fall of 2004. Basal area increments in the period before tethering were calculated by subtraction of the cross-sectional area in 1993 from that in 1998 and after tethering by subtraction of the cross-sectional area in 1999 from that in 2003. Similarly, the mean proportion of latewood prior to treatment (1993 to 1997) and after treatment (1999 to 2003) was averaged for the four radii.

Because trees growing at the under story of the plot would experience different wind regimes than those growing in the upper canopy stories, therefore, it was of interest to compare the height growth of the subordinate trees from those of dominant trees when wind-induced bending was changed. In this study, there was only a small sample of subordinate trees that could be collected from each plot (1 or 2 trees from each plot). However, to demonstrate how the

treatment affects the height growth of the trees growing at different canopy positions, the results from those few subordinate trees were also presented.

Sapwood hydraulic characteristics

Hydraulic permeability measurement of the stem sections was conducted using techniques similar to those described by Sperry et al. (1988) and Mencuccini et al. (1997). Of the 1 m stem section taken from tethering height, the top and bottom 30cm were cut and discarded when they still were frozen. An approximately 20cm section was cut from the rest of the section and used for permeability measurement. Those 20cm sections were primarily targeted to center on the 1m sections but subjected to slightly position adjustment to avoid the branch nodes. Samples were cut while frozen to prevent the introduction of embolism to the cut end. They were then thawed overnight while submerged in 10 mM oxalic acid in filtered (0.2 um) distilled water to suppress growth of bacteria and fungi. After thawing, the ends of the 20 cm section were planed with sharp low angled plane. Hydraulic permeability was measured with an apparatus described by Protz et al. (2000) that uses hanging water columns to generate a constant hydraulic head (16.7 kPa) across the stem section. Both ends of the stem section were fitted with rubber caps to a coupling attached to the apparatus. Permeability was measured with degassed water and outflow was determined with an electronic balance. Outflow perfusate temperature was recorded to correct for variations in water viscosity. Steady flow was usually observed after 5 min. Once it stabilized, the mean flow rate over the next 20 min was used to calculate permeability. Once the permeability measurement was completed, thin disks were cut at the both ends of the stem section and the boundary separating translucent sapwood to heartwood was marked with a pencil. The separated sapwood and heartwood area were determined using image analysis software (Sigma Scan Pro, SPSS Inc., Shicago, I11.).

Hydraulic conductivity (K; m s^{-1}) was calculated according to Darcy's law as:

$$K = \frac{Ql}{A_s \Delta\Psi} \qquad (3\text{-}1)$$

Where Q is the flow rate (m^3 s^{-1}) through a stem sample of length l (m) and conducting area of sapwood A_s (m^2), under a water potential difference $\Delta\Psi$ (m hydraulic head) along its length. Hydraulic conductivity is more typically expressed as hydraulic permeability, which accounts for viscosity of the permeate. Hydraulic permeability (k_s; m^2) was determined as:

$$k_s = \frac{Ql\eta}{A_s \Delta\Psi} \qquad (3\text{-}2)$$

Where η is the viscosity of water (Pa s).

Bending moment/ stress assessment

The stems of the trees were assumed to act as cantilever beams with one end anchored at the ground. Bending moment (M) produced from wind load was calculated as:

$$M = F * L \tag{3-3}$$

Where, F is wind load, which was assumed to act on the center of the crown as a point load (Dean and Long, 1986); L is the leverage which was measured from center of the crown to any point along the bole.

Because the axial stress caused by gravitation is a small component, it was neglected in the calculation of the total stress (Morgan and Cannell, 1994). The maximum bending stress (σ) experienced at the outer edge of the stem was calculated as:

$$\sigma = \frac{M * c}{I} \tag{3-4}$$

Where c is the radius of the stem; I is the moment of inertia for an object with a circular cross section (Neathery, 1982), which is:

$$I = \frac{\pi * D^4}{64} \tag{3-5}$$

D is bole diameter. Rearranging, it became:

$$\sigma = \frac{F * L * 32}{\pi * D^3} \tag{3-6}$$

For the control trees, the bending moment, and stress at tethering height (10m height) was calculated as:

$$M_{10} = F * L_1; \quad \sigma_{10} = \frac{F * L_1 * 32}{\pi * D_{10}^{\ 3}} \tag{3-7}$$

Where L_1 is the leverage from center of the crown to 10m height; D_{10} is the inside bark diameter at 10m height (Figure. 3-1 a).

Similarly, the bending moment, and stress at 1.3 m height for control trees was calculated as:

$$M_{1.3} = F * (L_1 + L_2); \qquad \sigma_{1.3} = \frac{F * (L_1 + L_2) * 32}{\pi * D_{1.3}^{\ 3}} \tag{3-8}$$

Where $D_{1.3}$ is the inside bark diameter at 1.3m height; L_2 is the distance between 10m height and 1.3m height.

The ratio of bending moments, and stresses at those two points was:

$$M_{1.3} : M_{10} = \frac{(L_1 + L_2)}{L_1} \; ; \qquad \sigma_{1.3} : \sigma_{10} = \frac{(L_1 + L_2) * D_{10}^{\ 3}}{L_1 * D_{1.3}^{\ 3}} \tag{3-9}$$

Because F is the same between M_{10} and $M_{1.3}$, and between σ_{10} and $\sigma_{1.3}$, it was cancelled out in the calculations, thereby avoiding the difficult problem of accurate estimate of F.

Using the same procedure, the ratio of moments/stresses in 1998 was also calculated for each of the five largest control trees. When the moment/stresses were calculated for the year of 1998, it was assumed that the length of the live crown was the same during the periods before and after installation of the roping and hence, bending moments/stress at the 10m height and 1.3m height was calculated accordingly.

Tethered trees were subjected to an external pulling force (P) at the tethering height countering the natural sway of the tree under wind load (Figure 3-1b). This force was derived by applying the force method to analyse statically indeterminate structures (Hibbeler, 1999):

$$P = 0.5F(3\frac{L_1 + L_2 + 1.3}{L_2 + 1.3} - 1) \quad \text{(see appendix for more detail of derivation)} \tag{3-10}$$

The bending moments and stresses at tethering and 1.3 m height were calculated as follows:

$$M_{10} = F * L_1 ; \; \sigma_{10} = \frac{F * L_1 * 32}{\pi * D_{10}^{\ 3}} \tag{3-11}$$

$$M_{1.3} = F * (L_1 + L_2) - P * L_2 ; \qquad \sigma_{1.3} = \frac{\{F * (L_1 + L_2) - P * L_2\} * 32}{\pi * D_{1.3}^{\ 3}} \tag{3-12}$$

The ratio of bending moments and stresses at 1.3 m height and tethering height was:

$$M_{1.3} : M_{10} = \frac{(L_1 + L_2) - L_2 * 0.5 * (3 * \frac{L_1 + L_2 + 1.3}{L_2 + 1.3} - 1)}{L_1} ;$$

$$\sigma_{1.3} : \sigma_{10} = \frac{\{(L_1 + L_2) - L_2 * 0.5 * (3 * \frac{L_1 + L_2 + 1.3}{L_2 + 1.3} - 1)\} * D_{10}^{\ 3}}{L_1 * D_{1.3}^{\ 3}} \tag{3-13}$$

Mean overall bending moment

The mean overall bending moment in 2004 was calculated by averaging the bending moments of each relative height from base of the stem up to tethering height for each tree.

The bending moments of those relative heights was calculated as:

For control trees:

$$M_{rht} = F*(L_1 + L_2 + 1.3 - H_c) \quad (3\text{-}14)$$

For tethered trees:

$$M_{rht} = F*(L_1 + L_2 + 1.3 - H_c) - P*(L_2 + 1.3 - H_c) \quad (3\text{-}15)$$

Where, M_{rht} (N · m) is the bending moment at those relative heights when H_c (m) is less than 10m; H_c is the height to each position on the stem; D_{rht} (cm) is the diameter at each relative height.

The wind force F (N) was estimated as:

$$F = 1/2 C_d \rho A U^2 \quad (3\text{-}16)$$

Where, C_d is the drag coefficient (dimensionless), which is determined by wind speed, ρ is the air density (kg/m^3), A is the frontal area (m^2), and U (m/s) is the wind speed (Mayhead 1973). Frontal area was replaced by leaf area in the calculation as it reported that frontal area is proportional to leaf area for lodgepole pine (Dean and Long, 1986). Given that control plot and tethered plot in each site had similar landform, stem density, and spatial distribution of trees, it was assumed that C_d, ρ, and U were the same between control and tethered trees in each site. The ratio of mean overall bending moment in 2004 between tethered trees and control trees was calculated by dividing the mean overall bending moment of tethered trees by that of control trees and therefore C_d, ρ, and U cancelled out.

Statistical analysis

This experiment was a randomized complete block design. Sites were treated as the random factor and treatment was treated as a fixed factor. Treatment effects on height increment, basal area increment, and proportion of latewood were analyzed using Proc MIXED (SAS Institute, 9.1, Cary, N.C.). As only three of the four stands were able to be sampled, the experiment had weak statistical power, therefore an α=0.1 was used for the experiment.

Results

Tethering resulted in a significant increase in height increment (P=0.02) during the six years after tethering, compared to the six years prior to tethering (Table 3-2). For the tethered trees, the mean ratio of height increment six years after tethering to six years before the tethering was 1.40 compared to a mean of 0.80 for the controls.

Tethered trees had decreased basal area increment at 1.3m height ($BAI_{1.3m}$) six years after tethering relative to six years before tethering compared to control trees (P=0.05, Table 3-2). This was opposite to the values at 10m height, where tethered trees had increased BAI_{10m} after tethering (P=0.06, Table 3-2). Along the bole, for all of the sites, the tethered trees added more wood higher up the stem in the period after tethering than the period before tethering, compared to the control trees (Figure 3-2). At 0.8 relative height, the tethered trees had a 20% to 65% gain in basal area after tethering compared to the period before tethering (Figure 3-2). At 0.1 relative height, basal area increment of the tethered trees decreased between 25% and 30% relative to the period before tethering. In contrast, the control trees showed no consistent change in allocation with height, before and after the period of tethering.

Tethering increased height growth in relation to average diameter growth along the stem $\Delta H / \Delta D$ (P=0.04, Table 3-2) compared to the control trees. Tethered trees had an increase in stem volume growth after tethering, but it was not statistically significant (P=0.12, Table 3-2).

Tethering treatment produced a higher proportion of latewood at tethering height (10m) relative to the proportion of latewood at 1.3m height, six years after tethering (P=0.01, Table 3-2). For the control trees, the proportion of latewood at 10m height was 31% less than that at 1.3m. In comparison, six years after time of tethering, the proportion of latewood for the tethered trees was 2.6% greater at the tethering height than at 1.3m height.

The ratio of bending stresses at 1.3m vs. 10m height was greatly affected by the tethering treatment (Table 3-3). For the control plots, the ratios were near 1 in both 1998 and 2003. In contrast, because the tethered trees received an extra pulling force at the tethering height to counter the wind force, the mean ratio of the stresses at 1.3 vs. 10 m height, across all of the sites, was reduced to around 0.340 in 1998 at the time of tethering to 0.260 by 2003. The mean overall bending moment of tethered trees was reduced to 38% of the control trees across the three sites. The ratio of $BAI_{1.3m}$ and BAI_{10m} was also affected by the tethering treatment (Table 3-3.). The average ratio of the $BAI_{1.3m}$:BAI_{10m} was 0.667 on tethered trees, compared to 1.190 for control trees.

Six years after webbing treatment, unlike the consistent increase of height growth observed on dominant webbed trees across study sites, the subordinate trees from webbed plots showed a

consistent decrease of height growth than that of six years before the treatment (Table 3-4). As a comparison, the height growth of subordinate trees from control plots did not show this pattern.

There was no significant difference of hydraulic permeability between the stems of webbed trees and control trees (Table 3-2). Hydraulic permeability tended to be higher for webbed trees at two sites, but it was lower than control trees at the third site.

Discussion

The results of this study show that tall trees that are declining in height growth will increase their height growth rates when the overall bending moment of the trees is reduced by tethering (Table 3-2). This strongly suggests that mechanical constraints play a crucial role in limiting height growth when trees grow taller. In spite of the increased bending moment at the tethering height relative to 1.3 m height, the mean overall bending moment of the tethered trees was only 38% of control trees. The reduced overall bending moment apparently eased the need for lateral stem growth to maintain the stability of the tree during wind, resulting in increased height growth relative to radial growth along the bole (Table 3-2). Increased height growth may also have been related to increased stem elongation (Telewski and Jaffe 1986a; Telewski and Jaffe 1981) and reduced C allocation to structural root growth anchoring the stem (Urban et al. 1994; Stokes et al. 1997; Stokes et al. 1995; Henry and Thomas 2002) when the bending moment acting on the stem was reduced. The fact, that trees growing in windy area are shorter than those from sheltered areas (Ennos 1997), shows good evidence supporting the hypothesis that increased bending moment limits height growth.

For both control and tethered trees, this study shows the allocation of wood along the bole of large, dominant lodgepole pine trees is strongly related to bending moment. Tethering resulted in decreased bending moment at the base of the trees and increased bending moment at the point of tethering and above (Table 3-3). This resulted in a corresponding increase in wood allocation to the upper part of the trees (Table 3-2, Figure 3-2), similar to reports by Jacobs (1954) and Burton and Smith (1972). The quantitative analysis of the ratio of bending moments at 1.3m vs 10m and the corresponding ratio of BAI at those two points on both control stems and tethered stems indicates that C allocation along the bole was very closely related to the bending moments applied to the bole (Table 3-3). If wood properties were also considered in the analysis (Table 3-2), there would likely be an even closer relationship between wood growth/strength and lateral force

applied. At the tethering height, tethered trees grew wood with a higher percentage of latewood than at the same height of the control trees (Table 3-2), clearly indicating a response to counteract the change in the location of bending moment by a change in both the amount and type of wood laid down along the stem. The mechanisms by which the bending moment influences cell growth and division of the cambium were reported to be related with changes in ethylene production (Telewski and Jaffe 1986b). The fact that the bending stress was relatively uniform at 1.3m, and 10m up the bole in the control trees (Table 3-3) lends strong support to the uniform stress hypothesis for allocation of wood in trees (Dean and Long 1986). It is demonstrated however, if the bending stress along the bole is changed experimentally, allocation of wood changes accordingly.

I found that the proportion of latewood at tethering height relative to 1.3 m height was increased as a result of tethering (Table 3-2). In the control trees there was a higher proportion of latewood at 1.3 m height relative to 10m height. In both the tethered and the control trees, the higher percentage of latewood developed at the point of higher bending moment, suggesting that trees invest in high-strength latewood to counter increasing bending moment as they become larger. My observation of an increased proportion of latewood as a result of tethering is counter to Burton and Smith's (1972) study which reported guying loblolly saplings resulted in increased latewood growth at the height of guying, but not the proportion of latewood. I speculate this different result might be because they concentrated on the latewood growth only at guying height, thus failing to note the accompany changes at 1.3 m height. It is also likely that their saplings were smaller in size, and were therefore subjected to less bending moment compared to the taller trees.

Studies have suggested that C allocation to height growth relative to radial growth is mainly affected by competition (Weiner et al. 1990; Weiner and Thomas 1992), competition plus vertical foliage profile of an individual plant (Yokozawa and Hara 1995), or internal plant variables such as nutrient status in foliage and stem (Thornley 1999). In this study, the light reaching the canopy of the trees was not affected by the tethering treatment, thus competition for light was unchanged before and after tethering, similar to studies by Telewski (1990) and Valinger (1992). Hence the shift of C allocation along the bole and the increased height growth of the tethered trees were a result of the altered bending moment caused by tethering. While others have attempted to separate the role of light competition and wind pressure on stem allometry (Holbrook and Putz 1989), only Mitchell (2003) and Henry and Thomas (2002) developed studies where shading and mechanical

stimulation were not confounded. Mitchell reported that shading did not have a strong effect on stem allometry comparing to bending effect on Douglas-fir seedlings grown for one summer. In contrast, Henry and Thomas found that light competition takes a dominant role influencing height-diameter allometry of an annual herbaceous plant. From this study it cannot be assessed how much the competition for light affects the stem allometry of the tall trees, however, it demonstrates, that bending moment has a strong effect on the C allocation along the bole of trees.

As both wind-induced bending and competition for light have been shown to have an effect on height growth relative to diameter growth, it would be also interesting to examine the height growth of trees growing at different canopy positions of the stand when the wind or light regimes of the stand was intervened. In this study, without changing light regimes, I found that reducing stem bending resulted in a large increase of height growth for dominant tethered trees (Table 3-3). Surprisingly, the height growth of subordinate trees from tethered plots showed an opposite growth trend; there was a large decrease over the six years of tethering treatment. It is not quite clear about the reasons behind this but I speculate that an increased wind penetration after tethering the trees could play a role to reduce the height growth of the subordinate trees. In addition, as only a small sample of subordinate trees was collected from each plot, the power of the test was weak and chance to commit a type II error was high. However, to evaluate the growth response of trees growing at different canopy positions following various wind-induced bending and shading treatments, I suggest a further study with a large sample size would be needed in the future.

This study indicates that allocation of resources to height and diameter growth along the stems of lodgepole pine trees can be explained by the wind forces applied to the various heights of the bole, providing empirical support for the uniform stress hypothesis (Dean and Long 1986), and the authors hypothesis that the upper height that a tree can reach is affected by mechanical constraints. As there was little difference in height and hydraulic permeability between tethered and control trees in this study, the hypothesis that height growth is limited by stem hydraulics (Ryan and Yoder 1997; Koch et al. 2004; Niklas and Spatz 2004), was not relevant in this study. When the bending moment was manipulated by tethering the trees at 10m height, thereby countering the wind force, the tethered trees added wood to the bole approximately in proportion to the bending moment along the bole after the tethering was applied. The overall reduction in bending moment of the tethered tree reduced the demands on the tree's resources to grow laterally to maintain mechanical stability, thereby allowing resources to be allocated to further height

growth.

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Table 3-1. Mean characteristics of the five largest trees from each control (C) and tethered (T) plot across sites in 1998, prior to plot establishment (Mean ± SE).

Plot	DBH(cm)	HT(m)	HT/DBH
TC_C	11.10±0.66	15.12±0.08	122.10±6.63
TC_T	12.82±1.07	17.25±0.49	121.70±7.41
AM_C	11.04±0.67	14.98±0.22	120.36±6.78
AM_T	10.85±0.77	14.91±0.28	122.20±10.36
RE_C	10.34±0.47	14.94±0.13	128.40±4.49
RE_T	11.70±0.61	14.67±0.50	110.94±4.71

Table 3-2. Means of response variables for mature lodgepole pine for tethered and control plots, 6 years before and after tethering treatment (Mean±SE; n=3)

Response variables	Tethered trees	Control trees	*P*-value
Ratio of height growth#	1.40±0.09	0.80±0.08	0.02
Ratio of BAI at 1.3m height*	0.77±0.05	0.93±0.08	0.05
Ratio of BAI at 10m height	1.46±0.15	0.91±0.06	0.06
Ratio of ΔH/ΔD†	1.35±0.11	0.98±0.14	0.04
Change in stem volume growth % ‡	0.14±0.09	-0.01±0.10	0.12
Change in proportion of latewood % §	2.63±3.37	-30.97±1.10	0.01
Hydraulic permeability ($10^{-12}m^2$)	2.06±0.11	2.35±0.22	0.37

Ratio of height growth is the ratio of height growth six years after tethering to the height growth six years prior to tethering

* Ratio of basal area increment (BAI) is the BAI of the period 99-03: BAI of the period 93-97 ($BAI_{99\text{-}03}/BAI_{93\text{-}97}$)

† Ratio of ΔH/ΔD is the ratio of height increment-average diameter increment along the bole (ΔH/ΔD) of the period 99-03: ΔH/ΔD of the period 93-97

‡ Change in stem volume growth is the change in stem volume growth (Svol) of the period 99-03 relative to the period 93-97 ($(Svol_{99\text{-}03}\text{-}Svol_{93\text{-}97})/Svol_{93\text{-}97}$)

§ Change in proportion of latewood is the change in proportion of latewood at 10m height relative to 1.3m height during the period of 99-03 ($(PL_{10}\text{-}PL_{1.3})/PL_{1.3}$, where PL denotes percentage of latewood)

Table 3-3. Ratio of bending moment (M) , bending stress (σ), basal area increment (BAI) at 1.3 m height to those at tethering height (10 m) in the year of 1998 (pre-tethering) and 2003, in relation to tethering (t) and control (c) treatments across the three sites (Mean±SE).

Plot*	$M_{1.3m}/M_{10m}$ in 1998	$M_{1.3m}/M_{10m}$ in 2003	$\sigma_{1.3m}/\sigma_{10m}$ in 1998	$\sigma_{1.3m}/\sigma_{10m}$ in 2003	$BAI_{1.3m}/BAI_{10m}$ 1999-2003
TC_C	3.68±0.12	3.27±0.08	0.971±0.076	0.991±0.084	1.117±0.084
RE_C	3.41±0.12	3.02±0.12	0.910±0.080	0.907±0.080	1.059±0.130
AM_C	4.80±0.26	3.76±0.12	0.968±0.083	0.946±0.087	1.389±0.107
TC_T	1.13±0.06	0.61±0.03	0.327±0.022	0.258±0.012	0.634±0.056
RE_T	1.15±0.19	0.74±0.11	0.313±0.047	0.260±0.040	0.746±0.098
AM_T	1.32±0.14	0.64±0.06	0.373±0.049	0.278±0.037	0.632±0.137

* TC is Two Creeks site; RE is Redrock site; AM is Amundson site.

Table 3-4. Height growth of dominant trees in relation to subordinate trees for both tethered plots and control plots, 6 years before and after tethering treatment (Mean±SE; n=3)

	Dominant trees	Subordinate trees	*P*-value
Ratio of height growth of tethered plot*	1.40±0.09	0.54±0.16	0.04
Ratio of height growth of control plot	0.80±0.08	0.87±0.13	0.57

* Ratio of height growth was calculated as the ratio of height growth six years after tethering to the height growth six years prior to tethering

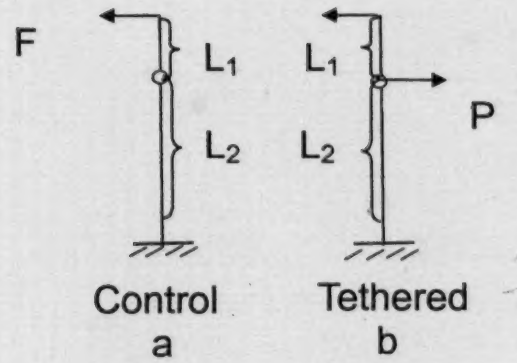

Figure 3-1.a. b. Dimensions and variables used in the calculations of the wind load and the pulling force acting on control trees and tethered trees. Where F is wind load; P is external pulling force; L_1 is the leverage from center of the crown to 10m height; L_2 is the distance from 10m height to 1.3m height.

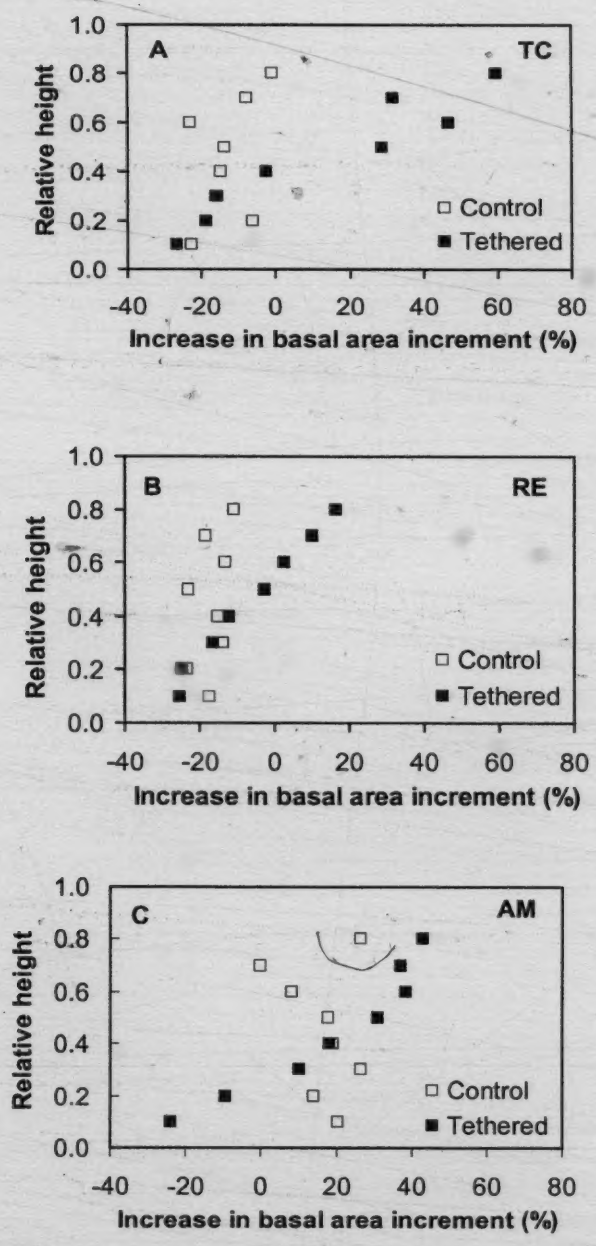

Figure 3-2. Mean increase in basal area increment of five dominant and co-dominant trees during the period of 99-03 relative to the period 93-97 $\{(BAI_{99\text{-}03}\text{-}BAI_{93\text{-}97})/BAI_{93\text{-}97}\}$ at various relative heights, of control trees and tethered trees at the site TC (A), RE (B) and AM (C).

Chapter 4: Bending moment governs the allometric scaling exponent for diameter-height of trees

Introduction

There has been a long search for the mechanisms that determine the scaling exponent of height to diameter of trees: $D \propto H^{\beta}$, or alternatively $H \propto D^{1/\beta}$, where D and H are diameter and height of the tree, respectively, and β is the allometric scaling exponent between diameter and height (Niklas 1995; O'Brien 1995; King 1996; Henry and Aarssen 1999; Sposito and Santos 2001; Niklas and Spatz 2004; Niklas et al. 2006). Over the past years, three models have been proposed based on the principles of mechanical design to describe the diameter-height allometric relationship. The elastic similarity model claims that the allometric scaling exponent β should be 3/2 so that the stem of the tree can maintain the elastic stability which prevents the stem from buckling under its own weight (McMahon 1973). Geometric similarity models consider β equal to 1.0 so that proportions of the tree remain constant through ontogeny (Rich 1986; Rich et al. 1986). When stress similarity for self-loading dictates the mechanical design of a tree, stem diameter is predicted to scale as the 2nd power of the stem length (β=2) (McMahon and Kronauer 1976). Each model assumes that a single design principle dictates this diameter-height relationship. However, numerous studies testing the scaling exponent found that none of those models holds true across different species or through their ontogeny (change in size) (Norberg 1988; Niklas 1995; O'Brien 1995; Sposito and Santos 2001; Niklas et al. 2006). Instead, a general trend of increasing β with increasing tree size or age has been detected (Niklas 1995; King 1996). The increase in β with size (age) has been suggested to relate to the increase in proportion of secondary tissue in older stems (Niklas 1995), but there likely are shifts in β between moderate and large tree trees, at times where there is only secondary growth. It also has been suggested that this age dependence of β is largely caused by neighbour effects; without the neighbour effects, the growth trajectories of diameter to height should be linear, not curved (Henry and Aarssen 1999). However, the allometry of open growth trees, eliminating the effects of neighbours, still shows that β is related to size (age) (Niklas 1995). Therefore, it remains unclear why β is size (age) dependent.

In this study I demonstrate that the scaling exponent between diameter and height is related to the change in mechanical perturbation applied to trees. Mechanical stability must be maintained over the life of the tree and resisting the bending moment produced from wind is

critical for tree survival (Schniewind 1962). Increases in crown size and height as trees grow taller increases bending moment at the base of the stem. Hence, to counter the increasing bending moment and prevent larger trees from breaking in the wind, more C is assigned to radial growth relative to height growth as they grow taller. The increase in radial growth relative to height growth as a result of increase in mechanical perturbation (bending moment) when tree grows bigger will increase the scaling exponent β. It has been shown that height growth vs. diameter growth is affected by the amount of bending experienced by a tree, for saplings (Telewski and Pruyn 1998) and large pines (Meng et al. 2006). However, there have been no studies to test that bending moment plays a crucial role in affecting the scaling exponent β, as trees growing bigger.

The objectives of this study were to test: (1) if allocation to bole girth relative to height growth increases with bending moment; (2) if the increase in bending moment with age results in an increase of the scaling exponent between diameter and height; and (3) if replacing β with a function of bending moment in the model $D \propto H^{\beta}$ will result in a better fitting than assuming a constant value of β when data are derived from trees with a wide range in size. From this study I show that β is related to the bending moment.

Materials and Methods

Data collection

The dataset was taken from pure, even-aged, fire-origin lodgepole pine stands 40 km south of Hinton, Alberta Canada. Five plots, adjacent to each other in a uniform stand, were thinned in spring of 1964 (8 years after fire) to densities of 7909, 3954, 1977, 988 and 494 stems per ha. Plots size varied with each density class, with each plot having 100 trees arranged in a 10×10 matrix. This group of five plots was replicated twice at each of three sites. The three sites were within 10 km of each other, all with similar landscape positions and wind exposure. The trees on these plots were tagged and their total height was recorded in the fall of 1964, following the first growing season after spacing. Trees were re-measured in 1966 and at subsequent 5-year intervals until 2001. At each measurement, total height, diameter at breast height (1.3m, DBH), crown width and crown length were recorded. Frontal area of each crown was calculated as the vertically projected area of the crown, assuming a conical crown shape.

A select group of trees were included in the analysis: First, in all cases I examined canopy trees, i.e. trees on the top half of the height-frequency distribution in each plot. I chose these taller

trees as they were well exposed to wind pressure. Second, I only included measurements of trees from 1981 and later. By this age, the base of the crown of all trees was above 1.3m, thus facilitating the calculation of bending moment acting at the breast height. Third, in my analysis of how β changes with tree age, I selected data from plots of the mid-density range (3954, 1977 and 988). As canopy trees from the lowest density plot and highest density plot varied substantially in size, these plots were excluded from the analysis (Table 4-1). Fourth, I randomly chose canopy trees measured during the interval of 1986 to 1991 for derivation of the relationship between the ratio of basal area increment to height growth (Ig/Ih) and bending moment (data from other intervals showed the similar results). Fifth, to fit and compare the proposed new model $D \propto H^{f(M)}$ (where, *f(M)* is a function of bending moment) and the old model $D \propto H^{\beta}$, which assumes a constant scaling exponent, 165 canopy trees were randomly selected across all levels of stand densities from each measurement from 1981 to 2001. To avoid autocorrelation issues, selection was without replacement, such that trees selected from one measurement could not be selected in subsequent measurements.

Bending moment estimation

The stems of the trees were assumed to act as cantilever beams with one end anchored at the ground. Bending moment (*M*) at breast height (1.3m) produced from wind force was estimated as:

$$M = F * L \qquad (4\text{-}1)$$

Where, *F* is wind force, which was assumed to act on the centre of the crown as a point load (Dean and Long 1986). *L* is the leverage measured from the centre of the crown to breast height.

Wind load *F* (m^2) was estimated as:

$$F = 1/2 C_d \rho A U^2 \qquad (4\text{-}2)$$

Where, C_d is the drag coefficient (dimensionless), which is determined by wind speed, ρ is the air density (kg/m^3), A is the frontal area (m^2), and U (m/s) is the wind speed (Mayhead 1973). As all the plots were close to each other and from the same area, and only canopy trees were sampled from each plot, I assumed the wind speed, C_d and ρ were the same for all the samples and set equal to unity for simplification of the calculations. Thus *F* becomes the relative wind load per unit wind speed.

Statistical analyses

Plots of log diameter against log height for data from each time of measurement showed a linear relationship. Reduced major axis (RMA) regression analyses were used to obtain the scaling exponent (β) and intercept ($\log\alpha$) by regressing the logarithmically transformed diameter ($\log_{10}$DBH) against height ($\log_{10}$Ht). The RMA procedure was chosen because it does not assume either independent or dependent variables to be fixed in the regression, which is more appropriate than ordinary least squares (OLS) regression which considers independent variable to be fixed (Henry and Aarssen 1999). Preliminary estimates of β and $\log\alpha$ were calculated using the approximation formulas $\beta = \beta_{OLS}/r$ and $\log a = \overline{\log_{10} DBH} - \beta\overline{\log_{10} H}$, where β_{OLS} is the scaling exponent obtained using OLS, r is the correlation coefficient; $\overline{\log_{10} DBH}$, $\overline{\log_{10} H}$ denote the mean of $\log_{10}$DBH and $\log_{10}$Ht, respectively (Niklas et al. 2006). OLS regression was completed using the Proc REG procedure of the SAS statistical software package (SAS Institute, Inc., 2004. Ver. 9.02). Five pairs of intercepts and scaling exponents were obtained from each of the five measurement times.

The mean bending moment was calculated for each measurement time, and the correlation coefficient between the scaling exponent and mean $\log_{10}$M was calculated. Analysis of residuals of basal area increment relative to height increment (Ig/Ih) vs. bending moment indicated that there was a trend of increasing variation with the increase of bending moment; therefore, both Ig/Ih and bending moment were also logarithmically transformed to reduce this trend. Non-linear regression (PROC MODEL, SAS Institute Inc. 2004. ver. 9.02) was used to fit the two models: $D \propto H^{\beta}$ and $D \propto H^{f(M)}$. Residual analysis and R^2 were used to judge the quality of the fit of the models. In addition, as two models contained different number of parameters, therefore, Akaike Information Criterion (AIC) was also calculated to compare the goodness of fit of the two models. AIC was calculated as:

$$AIC = n \cdot \ln(SSE/n) + 2p \qquad (4\text{-}3)$$

Where, n is number of observations; p is number of parameters; SSE is sum of square error.

Results

Basal area increment relative to height increment was linearly related to bending moment ($P<0.0001$, $r^2=0.58$, Figure 4-1). In trees with higher bending moment, there was increased growth in stem basal area relative to height.

The scaling exponent, i.e., the slope of the regression of log H vs. log DBH, increased with the age (size) of the trees (Table 4-2, Figure 4-2). Similarly, the bending moment also increased with the age (size) of the trees (Figure 4-2). There was a strong correlation between the average bending moment and the scaling exponent (r=0.98) calculated for each measurement time.

The new model incorporating bending moment in the scaling exponent had greatly improved fit to the data compared with the old model that assumed a constant scaling exponent (Table 4-3). These two models were fitted using data from the widest possible range of sizes and densities of dominant trees available in the data set. The R^2 of the model containing bending moment was 26 percentage points higher than that of the old model (Table 4-3). AIC of new model was far less than that of old model, indicating a much better fit of the new model (Table 4-3). Residuals analysis of the two models indicated there was an unbiased distribution of variance with the inclusion of bending moment into the new model comparing to that of the old model (Figure 4-3).

Discussion

As shown in previous studies (Niklas 1995; King 1996), I demonstrated that as trees increase in size (and age), the scaling exponent relating diameter to height also increases (Table 4-2, Figure 4-2). The fact that the scaling exponent, however, was strongly correlated to the bending moment of the trees (r=0.98) suggests that as trees grow in size, the scaling exponent is primarily governed by mechanical constraints related to bending moment. With the increase in bending moment as trees increase in crown size and height, there is increasing demand to invest C on radial growth relative to height growth (Figure 4-1) in order to maintain mechanical stability. This would directly result in the increase of the diameter-height allometric scaling exponent β. The increased basal area increment relative to height growth with the increase of bending moment shown from this study is consistent with the values achieved from the experimental studies testing the role of bending moment on C allocation in height and diameter for both saplings (Telewski and Pruyn 1998) and mature trees (Meng et al. 2006).

Since the scaling exponent is strongly affected by bending moment, and bending moment is subjected to dynamic change as trees grow, it is not unexpected that scientists have failed to find a single scaling exponent for diameter-height allometry by applying simple principles of mechanical design (Norberg 1988; O'Brien 1995; Sposito and Santos 2001; Niklas et al. 2006).

Even though this scaling exponent was found to be size- or age-dependent by some studies (Niklas 1995; King 1996), the mechanisms remained unclear. In this study, I have demonstrated that it is the increased bending moment as trees grow in size (age) that drives the increase of the scaling exponent. Thus, the allometric relationship of diameter to height of trees can be successfully described by principles of mechanical design.

Because the scaling exponent was shown to be a function of bending moment, incorporating bending moment into the model $DBH=\alpha_2 * Ht^{(\beta 1+\beta 2 * \log M)}$ achieved better prediction than the model with a constant β. The new model containing bending moment in the scaling exponent substantially improved the prediction of diameter from height than the old model, which assumed a constant scaling exponent (Table 4-3, Figure 4-3). Further, the increasing residuals with tree size noted for the old model was successfully corrected with the inclusion of the bending moment into the new model (Figure 4-3). The new model tended to be robust as data over a wide range of size was included to address the allometric relationship of diameter to height.

Studies have shown that both competition and wind loading have an impact on diameter-height allometry (Holbrook and Putz 1989; Henry and Thomas 2002; Mitchell 2003). Therefore, trees sampled from the upper canopy and bottom half of the canopy will tend to have different scaling exponents (Henry and Aarssen 1999) because of their different exposure to wind and their competitive status. In this study, in order to minimize the effect of light competition on diameter-height allometry, I restricted my samples only to the taller trees in the stand. Hence, primarily only wind-induced bending moment was assessed of its effects on diameter-height allometry. However, to fully evaluate the diameter-height allometry of trees, especially those below the canopy, I suggest that more information on wind in the understory will be needed to assess the bending moment of understory trees. Further, competition might also influence C allocation to diameter *vs*. height (Weiner et al. 1990; Weiner and Thomas 1992) and therefore have direct effects on the scaling exponent.

In conclusion, my study demonstrates that as trees grow in size (age), the increasing bending moment applied to the stems due to the wind force drives trees to allocate increased resource on radial growth relative to height growth, to efficiently counter the wind force and maintain the mechanical stability of the tree. This shift of C allocation causes the scaling exponent to increase with age. Thus, the allometric relationship of diameter to height of trees can

be successfully described by principles of mechanical design with the consideration of the bending moment. Revealing this mechanism can advance my knowledge on C allocation, diameter-height allometry and provide insights to the mechanisms that cause the trees to approach their upper height limit (Pennisi 2005; Meng et al. 2006; Ryan et al. 2006).

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Table 4-1. Characteristics of canopy trees sampled from plots at three density levels (3954, 1977, and 988 stems/ha) over repeated measurements.

MeasurementYear	Min. DBH (cm)	Max. DBH (cm)	Mean DBH (cm)	Min. height (m)	Max. height (m)	Mean height (m)	n
1981	3.8	19.0	9.7±0.1	4.5	10.2	6.7±0.1	805
1986	5.3	22.9	12.0±0.1	6.2	13.1	8.5±0.1	795
1991	5.8	25.9	13.6±0.1	7.6	14.3	10.1±0.1	816
1996	6.5	27.4	14.7±0.1	8.9	16.5	11.6±0.1	869
2001	6.2	29.2	15.6±0.1	9.9	17.3	12.5±0.1	751

Table 4-2. Summary of statistics of linear regression of $\log_{10}$DBH vs. $\log_{10}$Ht of canopy lodgepole pines from plots at three density levels (3954, 1977, and 988 stems/ha) over repeated measurements

Measurement Year	$\log\alpha$	β	r^2	n
1981	-0.78	1.65	0.68	805
1986	-0.96	1.76	0.53	795
1991	-1.22	1.98	0.53	816
1996	-1.40	2.14	0.48	869
2001	-1.37	2.09	0.45	751

logα=y-intercept of linear regression; β=slope of linear regression.

Table 4-3. Comparison of the fit of two models, DBH=a*Ht$^{\beta}$ and DBH=a1*Ht$^{(b1+b2*logM)}$, to data from canopy lodgepole pine trees randomly sampled without replacement from all levels of stand densities over repeated measurements.

model	a	β	$a1$	$b1$	$b2$	R^2	AIC*	n
DBH=a *Ht$^{\beta}$	0.77	1.23				0.61	1789	825
	p<0.01	p<0.01						
DBH=			9.68	-0.70	0.37	0.87	901	825
a1*Ht$^{(b1+b2*logM)}$			p<0.01	p<0.01	p<0.01			

DBH = diameter at breast height, Ht = tree height, and logM = logarithmically transformed bending moment. a, β, a1, b1, b2 are fitted parameters. $R^2 = 1 - \sum(y-\hat{y})^2 / \sum(y-\bar{y})^2$.

*AIC was calculated based on equation: $AIC = n \cdot \ln(SSE/n) + 2p$, where SSE is sum of square error, n is number of observations, p is number of parameters.

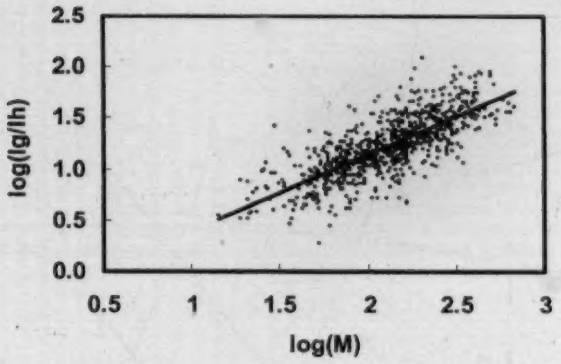

Figure 4-1. Logarithmically transformed basal area increment relative to height increment (log(Ig/Ih)) plotted against logarithmically transformed bending moment (log(M)) of canopy trees across three density levels during the period from 1986 until 1991. The line is the linear least-squares best fit line to the data (adjusted r^2=0.58, $p<0.0001$).

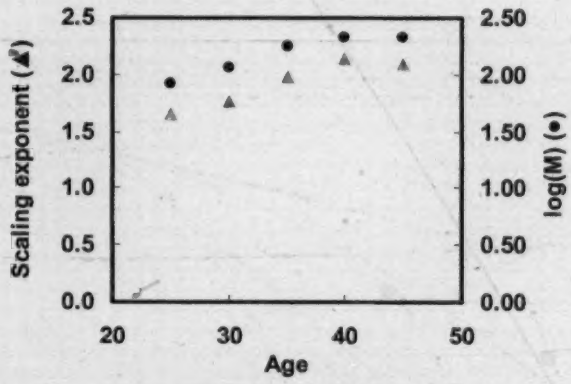

Figure 4-2. The changes over time in the scaling exponent (β) and the mean logarithmically transformed bending moment (log(M)) of canopy lodgepole pines sampled from plots at three density levels (3954, 1977, and 988 stems/ha).

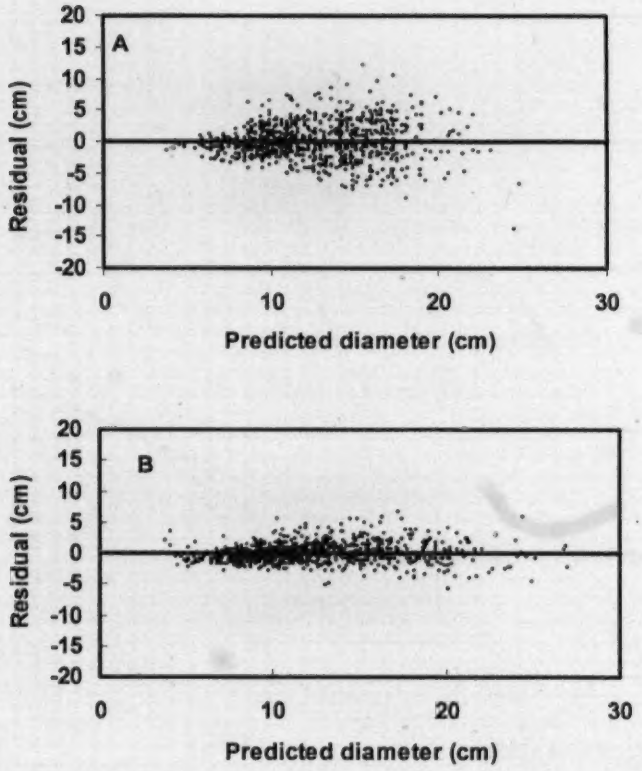

Figure 4-3. Residuals of fitting models DBH= α_1*Ht$^{\beta}$ (a) and DBH=α_2*Ht$^{(\beta 1+\beta 2*\log M)}$ (b) to data from canopy trees randomly sampled without replacement from all levels of stand densities over repeated measurements. DBH = diameter at the breast height; Ht = the tree height; logM = the logarithmically transformed bending moment. α_1, β, α_2, β_1, β_2 are fitted parameters.

Chapter 5: Bending moment serves as a predictor of basal area increment of lodgepole pine grown at various stand densities

Introduction

It is likely that selection pressure over evolutionary history has resulted in the basic geometry of trees conforming to mechanical principles. This allegation can be supported by the observation that trees effectively cope with the mechanical forces arising from their own weight and particularly from the dynamic loadings induced by wind-pressure (Jaffe 1973; King 1986; Mattheck 1991; Niklas 1998). When wind force acts on the crown of trees, it produces an increasing bending moment toward the base of the stem. To counter this bending moment and maintain mechanical stability, trees have shown great flexibility to reallocate their carbohydrate between aboveground and belowground structures (Henry and Thomas 2002; Stokes et al. 1997; Urban et al. 1994), and between radial growth and height growth (Meng et al. 2006; Telewski and Jaffe 1981; Telewski and Jaffe 1986; Telewski and Pruyn 1998). An increase in bending moment is followed by an increase in basal area growth to cope with this change (Meng et al. 2006; Metzger 1893). The amount of C assigned for basal area increment relative to height growth has been shown to be closely related to the bending moment of the trees caused by wind force (Meng et al. 2006) or other mechanical perturbation (Telewski and Pruyn 1998). As there are increased mechanical loading and bending moment as trees grow in height, it is anticipated that basal area increment of the tree will increase to counter these forces. The uniform stress theory (Dean and Long 1986; Metzger 1893) hypothesized that tree stems taper in a way to equalize the bending stress applied at the outer surface of the stem. Based on this idea, Dean (2004) has developed a useful model to describe the theoretical relationship between the basal area increment and the changes of the bending moment over a growth period. In Dean's model, however, the leaf areas at both the beginning and end of a growth interval are required for calculation of bending moment, which limits its application for prediction of growth. In addition, the effects of social position and stem density on wind pressure of each individual tree were neglected in Dean's model.

The objective of this study was to use the principles of mechanical design and exposure to wind to predict the basal area increment of different sized lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.) trees grown at different stand densities and site qualities.

Materials and methods

Data description

The Gregg River espacement trial was established by the Canadian Forestry Service in 1963 in the Gregg Burn, about 40 km south of Hinton, Alberta in pure, even-aged lodgepole pine stands that had regenerated naturally after a 1956 wildfire. Experimental blocks consisted of five plots, adjacent to each other in a uniform stand, were spaced in the fall of 1963 and the spring of 1964 at five levels: 1.1, 1.6, 2.3, 3.2, and 4.5 m, corresponding to stand density levels of 7907, 3954, 1977, 988, and 494 stems per ha. Two blocks were established in each of three site types: poor, medium, and good. The three sites were within 10km of each other, and subjected to the same wind exposure. The layout of the treatments was made by dividing each block into two and randomly assigning one half to a spacing level at the lower density. The remaining half of the block was again divided into two, and the spacing requiring the next lowest density was randomly assigned to one half. This procedure was repeated until all plots were assigned. Each plot included 100 trees arranged in a 10×10 square matrix. Plot area varied with spacing level. Starting in the fall of 1964, following the first growing season after spacing, the trees on these plots were tagged and their total height recorded. These trees were re-measured in 1966 and at subsequent 5-year intervals till 2001. At each measurement, total height, DBH, crown width, and crown length were recorded.

The wind load was assumed to act as a point load at the centre of the crown (Dean and Long 1986). To calculate the crown frontal area and leverage, trees were grouped into two categories. For those trees with the base of the live crown greater than 1.3m, crown frontal area was calculated as the vertically projected area of the whole crown, assuming a conical crown shape; leverage was calculated as the distance from centre of the crown to the breast height. For those with the base of the live crown below 1.3m, crown frontal area was the vertically projected area of the partial crown above 1.3m height, using the assumption of a conical crown shape; the leverage was the distance from centre of the same partial crown to the 1.3m height. As a high percentage of trees were recorded having disease problems at the measurement time of 1996 and 2001, data collected during those measurement times were excluded. For the rest of the data, a sample of 1000 trees was randomly selected across all levels of stand densities from measurement time 1971 to 1991 (Table 5-1). To avoid temporal autocorrelation issues, selection was without replacement, such that trees selected from one measurement would not be selected in the subsequent measurements. As only a small percentage of trees were sampled from each

measurement time, such that the spatial autocorrelation could also be neglected. For model validation, another sample of 1000 trees were randomly selected from the data not used in the model fitting. Similarly, this was done without replacement across the re-measurements. Those randomly selected samples over various measurement times were then fitted into the model for estimation of parameters. As a comparison, data from each measurement were also fitted to the model individually to predict growth over specific five-year intervals for same aged trees.

Zero plane displacement (*d*) is the height where wind speed reduces substantially and quickly approaches near zero, as wind penetrates the stands. Zero plane displacement is influenced by factors such as wind speed and atmospheric stability (Lo 1995), but for a range of uniform canopies, the value of *d* is approximated as 2/3 of the mean height of the stand (Oke 1987). To simplify the calculation in this study, it was assumed that trees with height below the zero plane displacement have no exposure to wind. Relative depth to the zero plane displacement (*RZPD*) was used to describe the relative position of each tree to the zero plane displacement. *RZPD* was calculated as the ratio of the height of an individual tree to 2/3 of the mean height of the stand (zero plane displacement). About 5% of the trees were shorter than 2/3 of the mean height of the stand; for these trees their RZPD was calculated as though they were equal to 2/3 of the mean height, i.e., RZPD = 1. Basal area increment (*BAI*) was calculated by subtraction of the basal area at the beginning of the interval from the basal area at the end of the interval, divided by the years of the interval. Site index (SI) was estimated for each plot by averaging the heights of the three largest DBH trees on a 0.03 ha basis (at least 3 trees were picked up from each plot) and then deriving the height at the total age of 50 years old (Huang et al. 2001). Predictor variables were taken at the beginning of the growth period. Edge trees from all plots were excluded from the development of the model.

Model development

The model was derived based on the principle of mechanical stability of the tree (Dean and Long 1986) that bending moment determines the proportion of C allocated for radial growth relative to height growth (Meng et al. 2006). The total C that a tree can produce is a function of crown size and site quality (SI). Tree height growth has also been shown to be related to the mechanical loading for both small trees (Larson 1965; Liu et al. 2003; Telewski and Pruyn 1998) and mature, large trees (Meng et al. 2006), therefore, basal area increment can be directly related to bending moment and SI.

$$BAI = f_1(M \cdot SI) \qquad (5\text{-}1)$$

Where, *BAI* is the average annual basal area increment over a five-year interval; *M* is bending moment at breast height (1.3m) produced from wind force, which is determined by:

$$M = F \cdot L \tag{5-2}$$

Where, *F* is wind force, which was assumed to act on the centre of the crown as a point load (Dean and Long 1986). *L* is the leverage measured from the centre of the crown to breast height.

Wind load *F* was estimated as:

$$F = 1/2 C_d \rho A U^2 \tag{5-3}$$

Where, C_d is the drag coefficient (dimensionless), which is determined by wind speed, ρ is the air density (kg/m^3), A is the frontal area (m^2), and U (m/s) is the wind speed (Mayhead 1973). As all of the plots were close to each other and from the same area, I assumed C_d and ρ were the same for all the samples.

Rearranging eq. (5-1), (5-2) and (5-3), eq. (5-1) became;

$$BAI = f_2(A \cdot U^2 \cdot L \cdot SI) \tag{5-4}$$

As wind exposure of each individual tree subjected is affected by stand wind speed, stand density and its relative depth to the zero plane displacement (Oke 1987), therefore,

$$U = f_3(U_l, RZPD, RD) \tag{5-5}$$

Where, *U* is local wind speed of each tree subjected to; U_l is the stand wind speed passing right over the top of the stand and it was assumed to be a constant in this study, as all the plots were within the same area; *RZPD* is the relative depth to the zero plane displacement; *RD* is the relative density of the stand. RD was calculated as: $RD=G/(Dq^{0.5})$, where *G* is basal area (m^2/ha) of the entire plot and *Dq* is the quadratic mean diameter. RD was used as a measure of stand density in this study as it contains the information of both the size and number of the trees within each plot (Curtis 1982).

Substituting eq. (5-5) into (5-4), the model became:

$$BAI = f(A \cdot L \cdot SI \cdot (RZPD, RD)) \tag{5-6}$$

The basal area increment was plotted against other independent variables to check for the trend and correlation of each variable to *BAI* (Figure 5-1). A non-linear model was proposed to predict *BAI* from *AL* (bending moment, expressed as *M* hereafter), SI, *RZPD* and *RD*.

$$BAI = aM^{b0} RZPD^{b1} RD^{b2} SI^{b3} \tag{5-7}$$

Where; a, b_0, b_1, b_2 and b_3 are estimated parameters; other variables as defined above.

As residual analyses indicated that there was a trend of increasing variance with the predicted

basal area increment, so a logarithmical transformation was applied to provide a homogeneous residual variance. After log transformation, the model became:

$$\log(BAI) = \log a + b_0 \log(M) + b_1 \log(RZPD) + b_2 \log(RD) + b_3 \log(SI) \quad (5\text{-}8)$$

In this study, the *M* was calculated as the product of crown frontal area and leverage, under the assumption of constant wind speed. However, to be able to distinguish *M* from conventional variables of crown size, and tree height that are normally applied in most growth models, a theoretical relationship between *M* and stem size of trees was also tested.

$$DBH = a \cdot M^b \quad (5\text{-}9)$$

Where *DBH* and *M* were defined before; *a, b* are parameters. A theoretical value of 0.33 should be held for parameter *b*, based on the principles of mechanical design (Dean and Long 1986).

Statistics analysis

Linear ordinary least square analysis was used (SAS Institute, Inc., 2004. ver. 9.02) to fit Equations (5-8) and (5-9) to the data set. Correlation of determination (R^2) and root square mean error (RSME) were used to judge the goodness of the fit. The variance inflation factors (VIF) were applied to check the multicollinearity of all independent variables included in the model. If an independent variable had a VIF greater than 5 and showed strong correlation with bending moment, it was then excluded. For other correlated independent variables, whichever had less explanatory power was dropped. Residuals of fit were plotted against the predicted log basal area increment and untransformed basal area increment to check the bias of the variance distribution.

Results

The parameter *b* (b=0.328) was not significantly different from theoretical value 0.33 for eq. (5-9), when fitting data collected from various densities and ages in this study ($P<0.0001$, $R^2=0.91$), suggesting that *M* can be reliably referred to as a measure of bending moment for lodgepole pine.

Of the total variation of basal area increment, 74 percent can be explained by my model when fitted to data pooled over the range of stand ages from 15 to 35 (Table 5-2). Parameter estimates for all four variables included in the model were significant (Table 5-2). BAI was positively related to bending moment, relative depth to zero plane displacement and site index (Figure 5-1, Table 5-2) and negatively related to stand relative density (Figure 5-1, Table 5-2).

The variance inflation factors were all below 5 (Table 5-2), i.e., the critical value suggested by Van Laar (1991), indicating a negligible multicollinearity among the predictors. Plotting residuals against predicted values showed no bias in their distribution after BAI received log transformation (Figure 5-2).

When the model was fitted to predict BAI of same-aged trees over discrete five year intervals, the models explained 70 percent to 77 percent of the total variation of basal area increment (Table 5-3). As SI showed strong correlation with bending moment, it was excluded in the regressions. In all cases, bending moment and stand relative density significantly affected BAI (Table 5-3). Relative depth to zero plane displacement tends to have no effect on BAI at the early stages, but positively affected BAI when stands grew up (Table 5-3).

Testing the model using validation data showed that the model behaved reasonably well (Figure 5-3). Estimated parameters for the simple linear model $y_i = a + b\hat{y}_i$, where $y_i, \hat{y}_i$ were observed log BAI and predicted log BAI respectively, were: a=0.0120 b=0.9868 (P=0.0001). The null hypothesis of a=0 and b=1 was accepted based on the joint statistical test described in Judge et al. (1988). The R^2 between the observed log BAI and predicted log BAI was 0.76.

Discussion

By applying the principles of mechanical design, the model I proposed in this paper shows a good prediction of basal area increment using variables related to bending moment and exposure to wind (Table 5-2). When separate models were fit over specific stand ages, there was a close fit of the model (Table 5-3). This strong relationship between bending moment and radial growth shown in my model is consistent with those from experiments that tested the role of mechanical perturbation on radial growth by shaking, flexing, rubbing or wind exposure of either small trees (Larson 1965; Liu et al. 2003; Telewski and Jaffe 1986; Telewski and Pruyn 1998) or large trees (Jacobs 1954; Meng et al. 2006). My model builds upon the principles outlined by Dean (2004), adding several critical components, such as relative exposure of each individual tree and stand density. This allows an implicit simulation of the impacts of wind exposure on the basal area growth of each tree within a stand. The theoretical value of the exponent of 0.33 between DBH and bending moment tested in Dean and Long's study (1986) was confirmed using my data; this supports the principle that crown frontal area (A) and leverage from the mid-point of the crown can be used to estimate bending moment (also used by Dean (2004)), without the actual

measurement of wind speed. In this study, I showed that bending moment at the start of the growth interval was the strongest variable related to growth over a five-year interval. Site index also enters the model when BAI was modeled over a range of stand ages. Including site index into the model added a small increase in the goodness of fit of the model after M, RZPD and RD were in the model, thereby relating to the total C a tree may potentially produce, over and above the influence of crown size.

The variables used for calculation of bending moment in this study, i.e., crown size, stand relative density, relative depth to the zero plane displacement, have been used to describe the degree of competition to which a tree has been subjected. It has been assumed that competition for light determines the proportion of carbohydrate allocated to radial growth relative to height growth (Weiner et al. 1990; Weiner and Thomas 1992). Inclusion of a competition index, especially one that incorporates crown-related variables, into the growth model tends to improve the prediction (Brown et al. 2004; Cole and Lorimer 1994; Larocque 2002; Ottorini et al. 1996; Sharma et al. 2002; Wyckoff and Clark 2005). However, recent studies have shown that bending moment produced from wind also has a large effect on C allocation (Henry and Thomas 2002; Holbrook and Putz 1989; Meng et al. 2006; Mitchell 2003). Hence, incorporating effects of both shading and bending moment should allow a comprehensive assessment of the amount of C assigned for radial growth. This makes it possible to simultaneously simulate the effects of both shading and bending. Further more, the new model is useful for prediction of basal area increment over a wide range of stand densities.

In this study, I do not have direct data on the force of the wind applied to the crowns for each individual tree. Relative depth to the zero plane displacement (Oke 1987) and stand density were used as a surrogate for wind exposure and the force applied. Shorter trees and those sheltered by neighbours would experience reduced exposure to wind than relatively tall trees in open stands. This assumption is consistent with what has been shown by the model fitting, judged by the signs of the parameter estimation (Table 5-3). However, I have also noticed that relative depth to zero plane displacement tended to be a weak predictor in the models for prediction of growth for the younger age classes (Table 5-3). I postulated that this might be due to the fact that these stands were relatively uniform in height at early stages (judging by the standard deviation of tree height) which would diminish the importance of the relative position of each individual tree as an explanatory factor.

In the graph of residuals analysis, an unbiased band of residuals scattered randomly around the zero line can be observed (Figure 5-2.b). However, even though the residuals showed constant variance and zero mean, there was a slight predominance of positive residuals shown in the graph. This result may be unsatisfactory from a theoretical point of view, but it was assumed that the applied linear regression technique was sufficiently robust to be able to produce reliable estimates (Vanclay 1994). When the dependent variable is logarithmically transformed, a transformation bias is produced. Although it was very small, this bias was corrected by adding half the residual mean square to the right hand of the eq. (5-8) before taking its exponent.

The model was successfully validated by using the excluded data after model construction. As this validation data came from the same study plots as the original model, therefore, it is still not a truly independent test (Monserud and Sterba 1996). When testing my model with an independent datasets, however, difference in the average wind speed between the two dataset would need to be accounted for.

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Table 5-1. Statistics of lodgepole pine trees sampled across wide range of stand densities and site qualities over repeated measurement without replacement from Gregg espacement trial (S.E.=standard error)

Variable*	Mean	Minimum	Maximum	S.E.	N
DBH (cm)	7.1	0.8	21.6	0.1	1000
HT(m)	5.0	1.4	11.2	0.1	1000
BAI(cm^2)	7.1	0.06	27.77	0.16	1000
L(m)	1.90	0.1	6.2	0.1	1000
A(m^2)	6.84	0.01	46.53	0.22	1000
RZPD	1.50	1.00	2.50	0.01	1000
RD	2.79	0.05	12.22	0.08	1000
SI	21.2	13.4	28.8	0.1	1000

* Where, DBH is diameter at breast height; HT is tree height; BAI is basal area increment; L is leverage (distance from centre of the crown to breast height); A is crown frontal area, calculated as the vertically projected crown area with an assumption of conical crown shape; RZPD is relative depth to the zero plane displacement, calculated as the ratio of tree height to 2/3 of the average height of the plot; RD is the relative density; SI is the site index, calculated on a plot basis.

Table 5-2. Parameter estimates and related statistics for fitting model: $\log(BAI) = \log a + b_0 \log(M) + b_1 \log(RZPD) + b_2 \log(RD) + b_3 \log(SI)$ using data sampled across wide range of stand densities and site qualities over repeated measurement without replacement from the Gregg espacement trial.

Variable*	Parameter	Estimate	S.E.	*P*	VIF	R^2
Intercept	a	-1.12571	0.13500	<0.0001		0.74
log(M)	b_0	0.22745	0.01001	<0.0001	3.48	
log(RZPD)	b_1	1.01631	0.09633	<0.0001	1.54	
log(RD)	b_2	-0.41307	0.02135	<0.0001	2.72	
log(SI)	b_3	1.24196	0.09758	<0.0001	1.87	

*Where; *M* is bending moment; *RZPD* is the relative depth to the zero plane displacement; *RD* is the relative density; SI is site index, estimated based on plot basis; VIF is variance inflation factor.

Table 5-3. Statistics and parameter estimates of fitting model: $\log(BAI) = \log a + b_0 \log(M) + b_1 \log(RZPD) + b_2 \log(RD)$ using data sets sampled across a wide range of stand densities and site qualities from the Gregg espacement trial at different ages of the stands.

Age of the stand	Variables	Estimates of parameters (mean±SE)	RMSE	R^2
15-20	Intercept	0.784±0.017	0.178	0.702
	log(M)	0.299±0.007		
	log(RZPD)	-0.195±0.079		
	log(RD)	-0.326±0.012		
20-25	Intercept	0.690±0.012	0.176	0.771
	log(M)	0.370±0.007		
	log(RZPD)			
	log(RD)	-0.520±0.013		
25-30	Intercept	0.525±0.016	0.193	0.753
	log(M)	0.417±0.011		
	log(RZPD)	0.420±0.087		
	log(RD)	-0.719±0.017		
30-35	Intercept	0.362±0.026	0.195	0.752
	log(M)	0.505±0.016		
	log(RZPD)	0.271±0.103		
	log(RD)	-0.764±0.021		

Where; *M* is bending moment; *RZPD* is the relative depth to the zero plane displacement; *RD* is the relative density. All parameters listed are significant at 0.05 level.

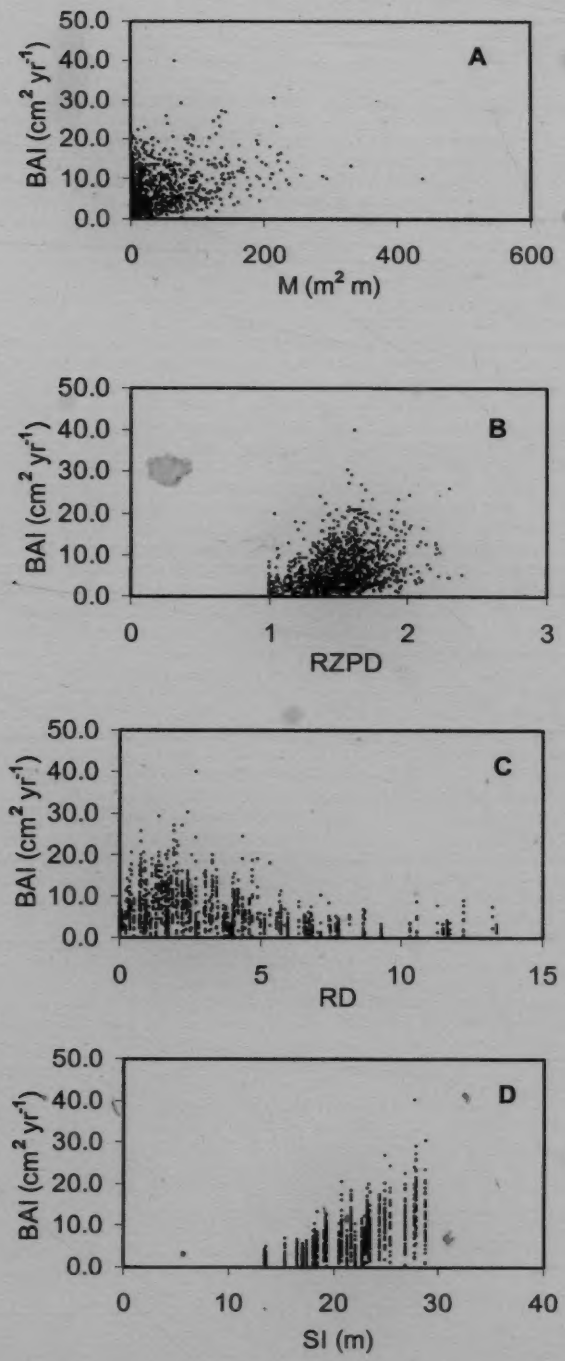

Figure 5-1. Scatter plots showing the basal area increment plotted against bending moment (M) (A), relative depth to zero place displacement (RZPD) (B), stand relative density (RD) (C), and site index (SI) (D).

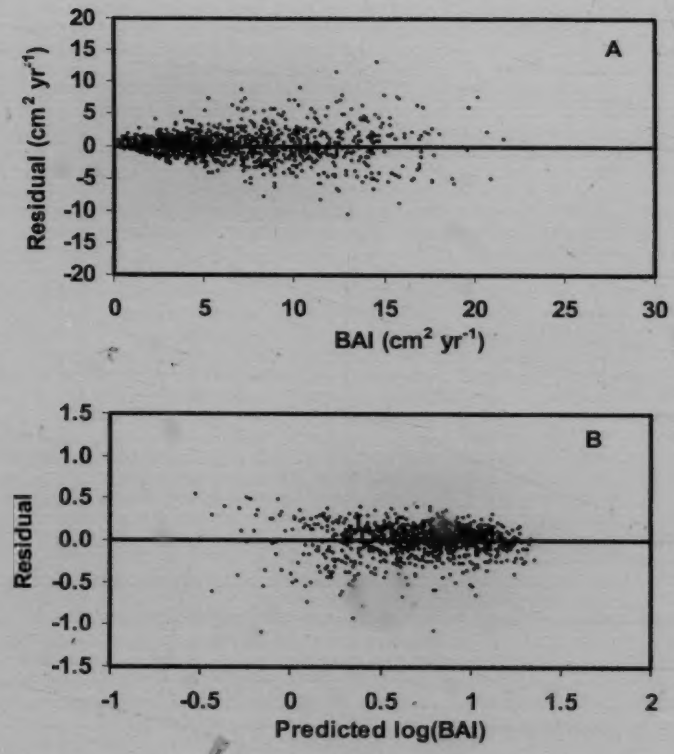

Figure 5-2. Residuals of fitting eq. (5-7) (A, data without transformation) and eq. (5-8) (B, data with log transformation) using lodgepole pine trees sampled across various stand densities, site qualities and ages from Gregg espacement trial. Residuals were calculated as the subtraction of observed values to predicted values; log(BAI) is the logarithmically transformed basal area increment.

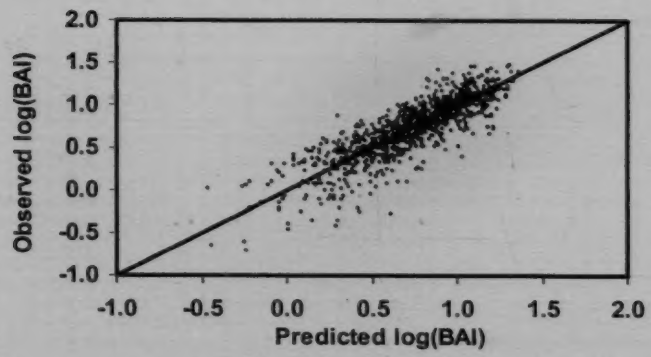

Figure 5-3. Predicted log (BAI) vs. observed log (BAI) of validating equation (5-8) using 1000 trees sampled from excluded data after model construction; log (BAI) is the logarithmically transformed basal area increment.

Chapter 6: Modeling crown volume of lodgepole pine based upon the uniform stress theory

Introduction

Because tree crowns are the source of carbohydrates from photosynthesis, the size of tree crowns and related variables are of interest to modelers of forest growth, competition and stand dynamics. Crown size is an important variable because it serves as a good indicator of the vigor of the tree and the accumulation of all of the factors that affected growth over stand development. Crown size is also a promising variable in some measure of competition (Daniels et al. 1986; Biging and Dobbertin 1995), different models for mortality prediction (Hasenauer and Monserud 1996), as well as stem growth prediction (Wykoff 1990; Cole and Lorimer 1994; Monserud and Sterba 1996; Wyckoff and Clark 2005). Because of its close link to leaf area, crown size serves as a good predictor of leaf area (Kenefic and Seymour 1999; Roberts et al. 2001). Studying crown dimensions also enables the estimation of crown shyness, the empty spaces surrounding tree crowns not attributable to mortality, which is believed to lead to reduced leaf area and productivity as stand ages (Rudnicki et al. 2001; Rudnicki et al. 2003; Meng et al. 2006b).

Considering the potential difficulty to directly measure the crown related variables in the field, there were great efforts involved to predict crown dimensions using commonly measured tree level and stand level variables. Stem diameter was considered the strongest variable to predict the crown radius as there is a close allometric relationship between the two variables (Krajicek et al. 1961). Other estimates incorporated tree or stand level variables such as tree height, crown length, live crown ratio, competition index, stand density and topography into the model (Hasenauer and Monserud 1996; Gill et al. 2000; Bechtold 2004). However, in addition to the increased complexity with the inclusion of more predictor variables in the model, the majority of the past work primarily focused on the prediction of live crown ratio (Hasenauer and Monserud 1996), or crown width (Gill et al. 2000; Bechtold 2004); work to directly predict the crown volume is rare.

In this study, I develop a new model, based on the uniform stress theory, to predict the crown volume of lodgepole pine. Uniform stress theory states that stems of trees taper to equalize the bending stress produced from wind drag acting on the crown (Metzger 1893; Dean and Long 1986). Therefore, there is a close linkage between the diameter of the stem and the bending

moment applied at that point (Dean and Long 1986; Dean 2004; Meng et al. 2006a). The amount of bending moment applied at breast height as a result of wind drag is a function of crown dimensions, leverage (the distance from the center of the crown to the breast height) and wind speed. Given the diameter at breast height (DBH), leverage and wind speed, the crown dimensions can be predicted.

The objective of this study was to develop a new model to predict crown volume of lodgepole pine (Pinus contorta var. latifolia Engelm.), based upon principles derived from the uniform stress theory. As crown radius is one of dimensions of crown volume, and has more difficulty to measure in the field than crown length, therefore, the second objective was to build a model for prediction of crown radius by using the inherent relationship between crown size and diameter, leverage and wind speed, according to the principles of mechanical design.

Materials and Methods

Wind speed estimation

Mean wind speed for each plot was estimated from the Canadian Wind Energy Atlas (CWEA), a large scale, high resolution wind energy simulation program developed by Environmental Canada in 2004. CWEA was designed to assess wind energy potential for any geographic locations across all Canadian territories. It was built based on statistical-dynamical downscaling methods (Frey-Buness et al. 1995) by combining long-term global climate data, high-resolution terrain data and advanced 3D high-resolution atmospheric modeling. The output of the CWEA includes mean wind speed, wind roses and wind energy. Given the coordinate of each location (longitude, latitude) across Canada, the mean wind speed can be estimated from the user-friendly interface of CWEA (more information is available at: http://www.windatlas.ca).

Model development

The uniform stress theory (Metzger 1893; Dean and Long 1986) states that trees adjust the taper of their stems to equalize the maximum bending stress experienced at the outer surface of the stem. This assumes that stem acts like a cantilever beam with one end firmly anchored in the ground with bending stress σ defined as:

$$\sigma = Mc / I \qquad (6\text{-}1)$$

Where, c is the radius of the cross-section; and I is the moment of inertia (Neathery 1982),

which is calculated as:

$$I = \pi DBH^4 / 64 \quad (6\text{-}2)$$

Where, DBH is the stem diameter at the breast height. M is the bending moment, calculated as the product of wind load (F) and leverage (L), which is the distance measured from the center of the crown to the breast height in this study. Center of crown was defined here as the point bisecting the crown length of the tree. The wind load is assumed to be a point load acting on the center of the crown (Dean and Long 1986). It is estimated as a function of crown frontal area and wind speed (Mayhead 1973):

$$F \propto CFA \cdot U^2 \quad (6\text{-}3)$$

Where, CFA is the crown frontal area; U is the wind speed.

Because crown frontal area represents two of the three dimensions in crown volume (CVOL), rearranging the equation (6-1), (6-2) and (6-3), we got:

$$CVOL = f(DBH, L, \sigma, U) \quad (6\text{-}4)$$

Since wind exposure of each individual tree subjected is affected by stand wind speed, stand density, and its relative depth to the zero plane displacement (Oke 1987), therefore,

$$U = f(U_s, RZPD, RD) \quad (6\text{-}5)$$

Where, U is tree level wind speed of each tree subjected to; U_s is the stand level wind speed passing right over the top of the stand; RZPD is the relative depth to the zero plane displacement; RD is the relative density (Curtis 1982).

With σ assumed to be constant (Dean and Long 1986), substituting eq. (6-5) into (6-4), the model for predicting crown volume became:

$$CVOL = f(U_s, DBH, L, RZPD, RD) \quad (6\text{-}6)$$

The similar procedure was also applied for building crown radius model. Because crown radius and crown length are two fundamental dimensions of crown volume, and crown length is a function of leverage L, therefore, rearranging eq. (6-6), the crown radius (CR) can be modeled as:

$$CR = f(U_s, DBH, L, RZPD, RD) \quad (6\text{-}7)$$

To further support the notion that DBH and L can be linked to crown volume through the principles of mechanical design in this study, a theoretical relationship between M and stem size of trees was also tested.

$$DBH = a \cdot M^b \quad (6\text{-}8)$$

Where a, b are parameters. A constant value of 0.33 should be held for parameter b, based on the principles of mechanical design (Dean and Long 1986).

Data description

Data sets were collected from permanent sample plots (PSP) established over various natural subregions across Alberta.

The PSP datasets were collected by Alberta Forestry Division during the past four decades. The PSPs were established in the early 1960's covering a wide range of densities, stand structures, species compositions, and site conditions throughout the forested areas of Alberta (Alberta Forest Service 2002). Plots established prior to 1981 at each location had a layout containing a group of four plots with the distance from the group center to the nearest corner of each plot is either 20.1m or 50.3m. Only one plot was established at each location after 1981. All standing trees with diameter at breast height (DBH) greater than 9.1cm were tagged, measured and tallied since the plot establishment. Repeated measurements were done on those trees at various intervals. Total tree height, and height to the base of live crown were recorded for all the live trees in each plot since 1998. Height to the base of live crown was defined as the point that separates the continuously branched portion of the tree and the part that has sporadic or no branching. Starting in 2000, a sample of trees was selected from each plot and crown radius at North, South, East and West directions was measured for each of the sampled trees. Crown radius measurement at each cardinal direction was estimated at the widest portion of the foliage looking up from the base of the tree. The sample size varied from 100 percent to 10 percent of the total tree numbers per plot depending on the density of each plot. A detailed description of the establishment and measurements of PSPs can be found in the Permanent Sample Plot (PSP): Field Procedures Manual (Alberta Forest Service 2002).

Only plots contained crown size measurement for lodgepole pine trees were selected for model development. For each lodgepole pine, crown radius was averaged from four crown radii measured at four cardinal directions. Crown volume was calculated based on measured crown length and mean crown radius, assuming a conical crown shape (a shape typical for lodgepole pine). The wind load was assumed to act as a point load at the centre of the crown (Dean and Long 1986). To facilitate the calculation of bending moment, only trees with height to base live crown greater than 1.3m were included. There were a total of 3480 lodgepole pine trees from 159 plots used in this study (Figure 6-1).

Zero plane displacement (d) is the height where wind speed is assumed to reach near zero,

as wind penetrates the stands. Zero plane displacement is affected by factors such as wind speed and atmospheric stability (Lo 1995), but for a wide range of tree species, the value of d is approximately given at: d=2/3h, where h is the mean height of the stand (height averaged over all trees within a stand) (Oke 1987). Trees with height below the zero plane displacement were considered to have virtually no exposure to wind (Oke 1987). Relative depth to the zero plane displacement (RZPD) was used to describe the relative position of each tree to the zero plane displacement. RZPD was calculated as the ratio of height of each individual tree to 2/3 of the mean height of the stand. Any tree shorter than 2/3h had RZPD set to 2/3h.

Crown volume and crown radius were plotted against other independent variables to check for the trend and correlation of each variable to CVOL, and CR (Figure 6-2, Figure 6-3). Given the inherent exponential relationship between DBH and bending moment as shown in eq. (6-8), the following non-linear models was proposed to predict CVOL and CR from DBH, L, mean wind speed Us, RZPD and RD.

$$CVOL = a * U_s^{b0} DBH^{b1} L^{b2} RZPD^{b3} RD^{b4} \quad (6\text{-}9)$$

$$CR = a * U_s^{b0} DBH^{b1} L^{b2} RZPD^{b3} RD^{b4} \quad (6\text{-}10)$$

Residual analyses indicated that there was a trend of increasing variance with the predicted crown volume and crown radius; thus a logarithmical transformation was applied to provide a homogeneous residual variance. After log transformation, the models became:

$$\log(CVOL) = \log a + b_0 * \log(DBH) + b_1 * \log(L) + b_2 \log(RZPD) + b_3 \log(RD) \quad (6\text{-}11)$$

$$\log(CR) = \log a + b_0 * \log(DBH) + b_1 * \log(L) + b_2 \log(RZPD) + b_3 \log(RD) \quad (6\text{-}12)$$

Where; a, b_0, b_1, b_2, b_3 are parameters.

Statistics analysis

Proc MODEL (SAS Institute, Inc., 2004. ver. 9.02) was applied to fit the equation (6-8). Stepwise multiple linear regression (SAS Institute, Inc., 2004. ver. 9.02) was used to fit equations (6-11) and (6-12) to the data sets. The value of alpha was chosen to be 0.05 for independent variables to enter the model. Coefficient of determination (R^2) was used to judge the goodness of the fit. The variance inflation factors (VIF) were applied to check the multicollinearity of all independent variables included in the model. Residuals of the fit were plotted against the log bending moment to check the bias of variance distribution.

Results

Of the parameter estimates for eq. (6-8) (a=4.458, b=0.341), b was not significantly different from theoretical value 0.33 , when fitting eq. (6-8) using data from lodgepole pine trees and stands from across Alberta ($P<0.0001$, $R^2=0.80$).

For the model built for prediction of crown volume (eq. 6-11), all the predictor variables entered into the model significantly affected the goodness of fit of the model (Table 6-2). The five independent variables explained 70% of the total variation on crown volume (Table 6-2). DBH had the strongest correlation with crown volume: DBH alone explained 62 percent of the total variation. Inclusion of leverage and mean wind speed added moderate improvements to the fit of the model. There was virtually no gain in the fit of model from the addition of RZPD or RD. Therefore, we decided to not include those two variables in the final form of the model. Of the three predictor variables, leverage, and wind speed negatively affected crown volume while DBH was positively related to crown volume (Table 6-2).

For the estimate of crown radius (eq. 6-12), except RZPD, the other four predictor variables entered in the model (12) all significantly affected the crown radius (Table 6-3). Similar to the fitting of crown volume, DBH, L and mean wind speed were the variables that contributed most to the total variation of the crown radius and RD was excluded because of its minor contribution to the model. Crown radius was negatively related to L and mean wind speed, and positively related to DBH.

The variance inflation factors were all below 5 for each regression, a critical value suggested by Van Laar (1991), indicating a negligible multicollinearity among the predictors.

Residuals analyses of the regressions for both eq. (6-11) and eq. (6-12) showed no bias of the variance distribution over predicted values (Figure 6-4).

Discussion

Using DBH, L and wind speed as predictor variables, the proposed models derived based on the uniform stress theory, showed a good prediction of crown volume, and crown radius of

lodgepole pine trees sampled from stands over a range of stand sizes and stand conditions. This suggests that the relationship between bending moment and stem size of trees derived from mechanical theory is suitable for prediction of crown dimensions. My model was built based on the hypothesis that selection pressure has resulted in trees possessing the correct balance between crown size, bending moment, and stem size. This hypothesis is supported by past experimental studies which found that when bending moment was changed by staking, guying, or addition of sail to increase wind load, there was a corresponding changes of diameter of the stem to maintain the mechanical stability of the stem (Larson 1965; Valinger 1992; Stokes et al. 1997; Telewski and Pruyn 1998; Liu et al. 2003; Meng et al. 2006a,). The fact that the exponent b tested in eq. (6-8) was not significantly different from the theoretical value 0.33, provided additional support to the idea that D and L can be linked to predict crown volume through principles of mechanical design.

It is noteworthy that leverage negatively affected crown volume and crown radius in the model regression (Table 6-2), which is consistent with the expectation that given a similar diameter, a tree with long leverage tends to have a small crown size, in order to maintain the mechanical stability of the tree. Also, mean wind speed was negatively related to crown volume and crown radius in the models, a result which matches closely with the field observation; when other factors are similar, trees growing in windy areas tend to maintain smaller crowns, thereby displaying a smaller sail and reducing the probability of windthrow in strong winds. The effect of wind pressure on crown dimensions has been shown to be related to crown collisions (Long and Smith 1992, Meng et al. 2006b). Increasing crown collisions when trees grow taller not only induce inhibition of branch growth due to thigmomorphogenetic effects (Telewski and Jaffe 1981, Telewski and Jaffe 1986), but also directly abrade neighboring twigs, branches thereby resulting in crown shyness, i.e., the empty space surrounding crowns that is not attributable to mortality.

The inclusion of relative depth to zero plane displacement and stand relative density into the model resulted in virtually no improvement of the fit of the regressions. The does not fit the expectation from the principles of mechanical stability, where when DBH, L are equal, the trees growing in a lower canopy level or in dense stands should experience a reduced wind load which should allow them to develop larger crowns when compared to trees in the overstory or in dense stands (Mattheck 1991; Ennos 1997; Niklas 1997). Trees that are from lower canopy positions or from dense stands, however, will also have respond to these conditions by reducing their DBH relative to height (Wang et al. 1998; Liu et al. 2003). So in fact, the smaller DBH in these trees

below the canopy or in high densities stands already accounts for the sheltering effect from wind that occurs within a stand.

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Table 6-1. Summary of tree and stand variables of data sets sampled from lodgepole pine permanent sample plots across various natural subregions in Alberta.

Variable*	Mean	Minimum	Maximum	STD	N
DBH (cm)	20.8	1.1	52.5	8.3	3480
HT(m)	18.7	2.5	34.4	5.8	3480
CVOL(m^3)	10.48	0.02	235.86	14.89	3480
CR (m)	1.15	0.10	3.58	0.50	3480
L(m)	14.8	0.7	27.8	5.2	3480
U_s(m/s)	4.54	3.20	8.47	1.10	159
RZPD	1.71	1.00	4.71	0.36	3480
RD	9.60	3.01	93.18	4.78	159

*Where, *DBH* is diameter at breast height; *HT* is tree height; *CVOL* is crown volume, assuming a conical crown shape; CR is crown radius, averaged over four crow radii measured over South, North, East, and West cardinal directions; *L* is leverage, measured as the distance from centre of the crown to breast height; U_s is mean wind speed, estimated from Canadian Wind Energy Atlas; *RZPD* is relative depth to zero plane displacement; *RD* is stand relative density.

Table 6-2. Statistics and parameter estimates of fitting equations (6-11) using data sets sampled from lodgepole pine PSPs across various subregions in Alberta.

Variables*	Estimates of parameters (mean±SE)	Partial R-Square	Model R-Square	F value	Pr>F
Intercept	-1.001±0.068				
log(DBH)	3.014±0.053	0.620	0.620	5674.36	<.0001
log(L)	-1.362±0.057	0.052	0.672	548.76	<.0001
log(U_s)	-0.916±0.061	0.022	0.694	251.30	<.0001

*Where, *DBH* is diameter at breast height; *HT* is tree height; *CVOL* is crown volume, assuming a conical crown shape; *L* is lever length, measured as the distance from centre of the crown to breast height; U_s is mean wind speed, estimated from Canadian Wind Energy Atlas.

Table 6-3. Statistics and parameter estimates of fitting equations (6-12) using data sets sampled from lodgepole pine PSPs from Alberta.

Variables*	Estimates of parameters (mean±SE)	Partial R-Square	Model R-Square	F value	Pr>F
Intercept	-1.255±0.064				
log(DBH)	1.072±0.021	0.536	0.536	4011.96	<.0001
log(L)	-0.464±0.024	0.043	0.579	351.80	<.0001
log(Us)	-0.359±0.025	0.027	0.606	238.11	<.0001

*Where, DBH is diameter at breast height; L is lever length, measured as the distance from centre of the crown to breast height; Us is mean wind speed, estimated from Canadian Wind Energy Atlas.

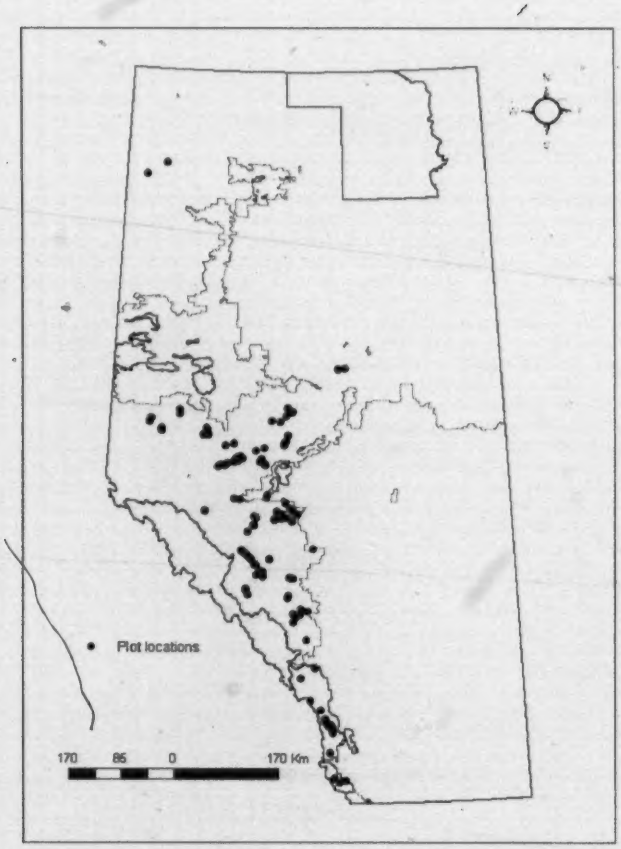

Figure 6-1. Plot locations of the sampled lodgepole pine PSPs (permanent sample plot) across various subregions in Alberta

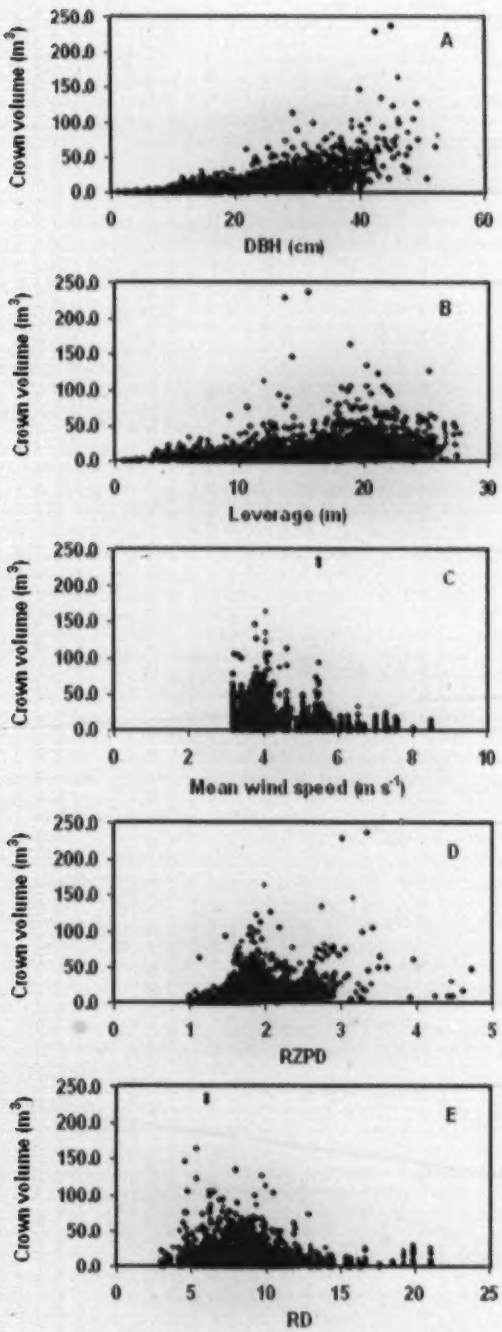

Figure 6-2. Scatter plots showing the crown volume plotted against diameter (A), leverage (B), mean wind speed (C), relative zero plane displacement (D) and relative density (E).

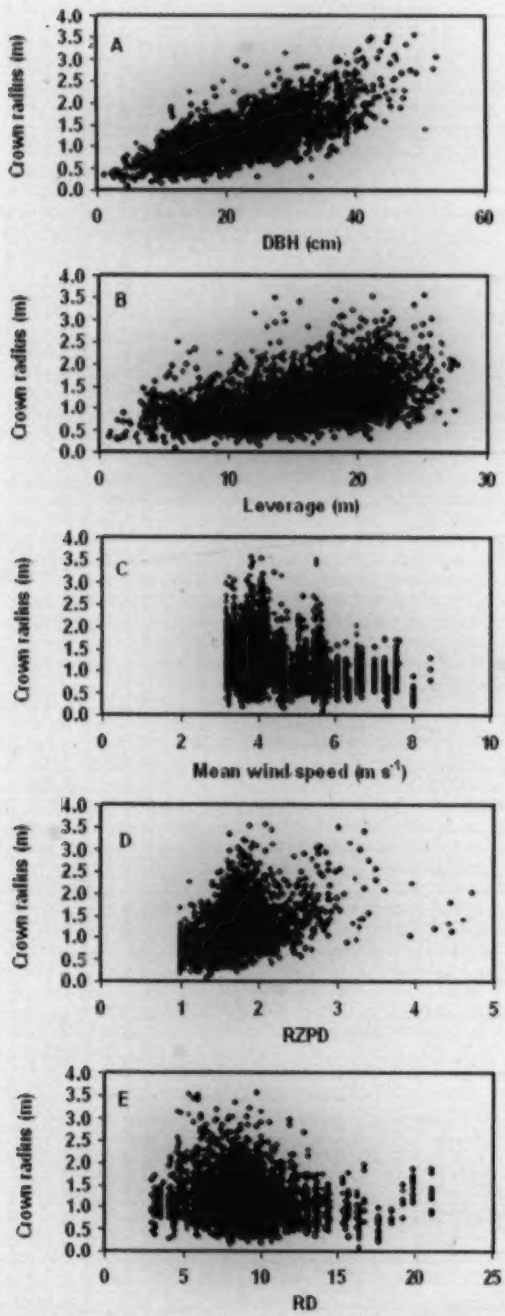

Figure 6-3. Scatter plots showing the crown radius plotted against diameter (A), leverage (B), mean wind speed (C), relative zero plane displacement (D) and relative density (E).

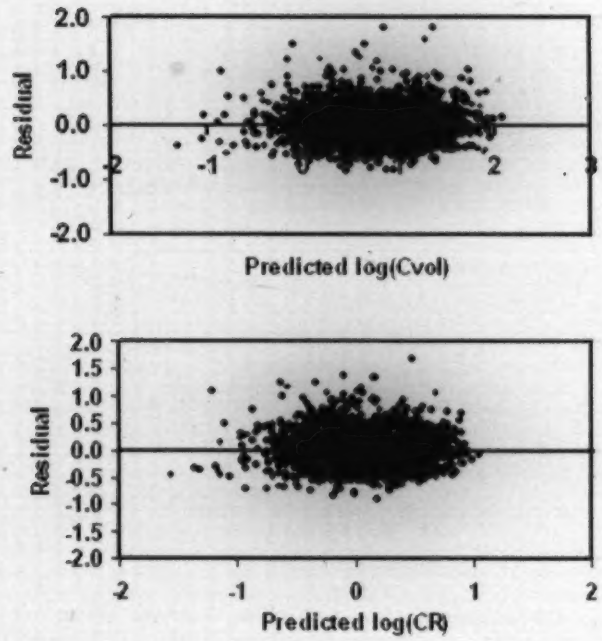

Figure 6-4. Residuals analyses of fitting equations (6-11) and (6-12) using data sets sampled from lodgepole pine PSPs (permanent sample plot) across Alberta (n=3480).

Chapter 7: Synthesis

Conclusions of this dissertation

By examining the effects of wind on crown and stem form, this study showed that crown collisions due to wind-induced tree sway play a significant role in affecting crown cover and leaf area of trees, supporting the hypothesis that crown shyness and the decline in leaf area are related to crown abrasions. It has also been found that bending moment, produced when wind force acts on the crown, has a big effect on height growth, as well as the stem form of large lodgepole pine trees. Further application of the relationship between bending moment and the stem growth achieved a good prediction of basal area growth and crown volume. Thus, this work has satisfied my research objectives:

1. Directly test the potential role of crown collisions on crown cover and leaf area of trees that experience crown shyness.
2. Test the mechanical constraints hypothesis on ultimate height growth by reducing the bending moment induced from wind force on large trees.
3. Quantify the relationship between the bending moment and the radial growth and wood property (ratio of latewood to earlywood) along the bole, to test the uniform stress theory.
4. Re-examine the allometry scaling exponent of diameter to height of trees based on the principles of mechanical design, with the consideration of the role of bending moment.
5. Model basal area increment by using the strong relationship between bending moment and radial growth.
6. Model crown volume based upon uniform stress theory.

To test the role of wind induced crown collisions on crown cover, groups of trees were tethered together in a web pattern at 2/3 height of the trees to minimize the impact of wind sway. Webbing achieved the goal of controlling wind effects in two different aspects: first, it prevented the direct physical abrasion of branches, and second, it refrained the touching and reduced the bending moment that would cause growth inhibition of new shoots due to thigmomorphogenetic effects (Telewski and Jaffe 1986; Telewski and Pruyn 1998). Even though those two aspects can not be separated, they all represent the effects of wind on crowns. Assessing crown cover changes by taking canopy photos at the beginning of the study and six years later is a novelty of this study.

This allows the direct comparison of the changes in crown cover by preventing crown collisions compared to that of the control. As light regimes were kept unchanged between webbed plots and control plots, thus, the big increase in crown cover after webbing was solely induced by reduction in crown collisions in this study. Further more, the examination of branch characteristics, leaf area density and crown symmetry found that crowns of webbed trees were more porous and symmetrical, compared to those of the unwebbed controls. These findings suggest that wind affects crown morphology. This is in contrast to the light hypothesis which suggests that branches grow preferentially into light-rich spaces, resulting in crown asymmetry (Koike 1989; Sorrensen-Cothern et al. 1993; Chen et al. 1996; Cescatti 1997).

The trees I studied were 15m tall at age of 50-55 years old. Those trees were declining in height growth and approaching their upper limit (24m at 180 years old, Huang et al. 2001). Therefore, reducing the bending moment induced by wind by tethering together those stems also enabled me to test my hypothesis that mechanical constraints plays a crucial role in limiting height growth of trees. My results showed, that reducing bending moment resulted in a large increase of height growth as a comparison to a substantial decrease of height growth on control trees. This supports the hypothesis that bending moment determines the carbon partitioning on height growth relative to radial growth for trees, in order to maintain the mechanical stability and avoid failure of the stem from wind. The quantification of bending moment at various heights of the stem by applying the force method (Hibbeler 1999) is another novelty of this study. It made possible to directly quantify the relationship between bending moment and the corresponding radial growth, wood property (ratio of latewood to earlywood). Further, the ratio of calculated bending stress at breast height and live base crown was close to 1 for control trees, supporting the uniform stress theory that tree stem grows in a way to counter the increasing bending moment toward the base of the stem and equalize the bending stress applied at the outer surface of the bole (Metzger 1893; Dean and Long 1986). My data indicate that there is a very close relationship of the radial growth plus the wood property and the amount of bending moment applied there.

The close relationship of bending moment and C partition among height and radial growth led me to another hypothesis: that bending moment determines the allometric scaling exponent of diameter-height of trees. Using data with repeatedly measured crown and stem dimensions, I found that with the increase of bending moment, there was increased C allocated for basal area growth relative to height growth. The scaling exponent of diameter-height increased with the age (size) of the tree and strongly correlated with bending moment. Thus, the scaling exponent which

has been failed to be described by past models by applying the principles of mechanical design, was demonstrated to be actually governed by bending moment from this study. It shows that the increasing bending moment plays an important role in driving the scaling exponent of diameter-height to increase with age/height.

My final thoughts in this study were to apply those results achieved from this study and others for the application of prediction of basal area growth and crown volume. In Chapter 5, by relying upon the strong relationship between bending moment and C partition in height growth and radial growth, I proposed a new model to predict basal area increment of trees. With the bending moment taken as a major predictor variable, and stand relative density and relative depth to zero plane displacement included as wind surrogate, new model achieved a good prediction of the BAI for trees grown at various stand densities. The close relationship of the bending moment and stem size derived from the uniform stress theory also made possible for me to propose a new model for prediction of crown volume.

Application

Productivity decline

My study confirmed that crown collisions play a big role in abrading off the edges of crowns and driving the loss of leaf area when stand ages. This reduction in leaf area due to crown collisions acts as a major factor contributing to the decline in productivity. The effects of crown collisions on reduced leaf area and productivity tend to be even manifest for trees growing in cold winters as there is increased brittleness of branches as air temperature drops below 0°C (Lieffers et al. 2001) and increased potential for crown abrasions (Roberson 1993). Hence, the understanding of the role of wind induced crown collisions on crown shyness will be able to aid foresters to improve the stand productivity by controlling the wind effects from manipulation of stand density or selection of tree populations that could efficiently resist the wind sway.

Stem form and wood property

This work also shows that wind affects tree stem form and wood property (ratio of latewood to earlywood) when it acts on the crown and produces a bending moment along the bole. Trees subjected to a wind force have more tapered stem than those from sheltered areas. The large bending moment also results in increased proportion of latewood to earlywood. Taking those effects into consideration can help forester manage trees with desired stem form and wood

property by controlling the wind load from taking thinning interventions or other treatments. Knowing that bending moment plays a big role in affecting the C partition and scaling exponent of diameter-height will also be beneficial to produce improved equations for better description of stem taper and diameter-height relationship.

Prediction of stem growth

Based upon the strong relationship between bending moment and radial growth, I proposed a new model to predict basal area growth of lodgepole pine. One advantage of this model is to be able to predict stem growth of trees grown at various stand densities. I anticipated this model will also be useful to predict growth response for trees receiving thinning treatment. Past models aimed to predict basal area growth of stands receiving thinning treatments primarily focused on the changes of competition (Sharma et al. 2002; Larocque 2002), or addition of a thinning response factor (Hawenauer et al. 1996). Some critical process like increased wind stress at the time after treatment is neglected. Studies have shown that increased wind exposure to a tree in the years immediately after thinning has substantial impact on C allocation on its radial and height growth (Liu et al. 2002). Therefore, a model included the effects of increased wind pressure following thinning treatments should be able to have a better prediction of thinning response.

New frontiers

Mechanical constraints on ultimate height growth of old trees

The mechanisms driving trees to approach their upper height limit needs further exploration, but is of particular interests to researchers (Pennisi 2005; Ryan et al. 2006). Numerous studies have shown that trees exhibit great flexibility to reallocate their C between height and radial growth to cope with the altered bending moment by shaking, staking, or guying treatment (Larson 1965; Valinger 1992; Telewski and Jaffe 1986; Telewski and Pruyn 1998; Meng et al. 2006). There is also a shift of C partition between above- and below-ground when changes of mechanical loading of the trees (Urban et al. 1996; Stokes et al. 1997). The scaling exponent of diameter-height governed by bending moment increases with age (size), indicating that there is increased C assigned for radial growth relative to height growth with the increase of bending moment. Those findings suggest that mechanical constraints due to increased bending moment when trees grow taller might play a crucial role in driving trees approaching their upper limit. From my study, it has demonstrated that mechanical constraints via bending moment profoundly affect the height growth of large lodgepole pine trees. Because those trees have not yet

approached the upper limit, it is still not the direct evidence to test the hypothesis. I suggest, some tall, old trees that approached the upper limit should be guyed to test the hypothesis that mechanical constraints govern the upper limit to height of trees.

Separation of the effects of competition and wind exposure on stem form

C partitioned between height and radial growth has been intensely studies. It has been suggested that C allocation to height growth relative to radial growth is mainly affected by competition (Weiner et al. 1990; Weiner and Thomas 1992), competition plus vertical foliage profile of an individual plant (Yokozawa and Hara 1995), or internal plant variables such as nutrient status in foliage and stem (Thornley 1999). Studies also have shown that mechanical perturbation due to shaking, flexing, or wind exposure played a big role in affecting C allocation between height growth and radial growth (Larson 1965; Telewski and Jaffe 1986; Telewski and Pruyn 1998; Meng et al. 2006). While there were attempts to separate the role of light competition and wind pressure on stem allometry (Holbrook and Putz 1989; Mitchell 2003; Henry and Thomas 2002), only Mitchell (2003) and Henry and Thomas (2002) have developed studies where shading and mechanical stimulation were not confounded. Mitchell reported that shading did not have a strong effect on stem allometry comparing to bending effect on Douglas-fir seedlings grown for one summer. In contrast, Henry and Thomas found that light competition takes a dominant role influencing height-diameter allometry of an annual herbaceous plant. As at least two growing seasons will be required to correctly assess the height growth of trees, those two studies were not able to truly evaluate the effects of wind pressure and competition on stem form of trees. Therefore, a long term study designed to separate the role of competition for light and wind pressure on stem allometry of trees tends to be necessary in the future study.

Environmental stress and C allocation

As important ecological and environmental factors, water, nutrient, light, and wind have shown to greatly affect growth and carbohydrates partitioned among different parts of the plant. Plants growing in infertile soils or experiencing drought conditions have increased root growth (Comeau and Kimmins 1989; Gower al et. 1996). Competition for light has been found to drive plants to increase height growth relative to radial growth (Weiner et al. 1990; Weiner and Thomas 1992). In terms of wind effects, numerous studies have shown that changing wind load by means of addition of sailing, guying or staking had great effects on C partitioned between underground and aboveground (Stokes et al. 1997; Urban et al. 1994; Henry and Thomas 2002), between leaf

area and stem growth (Telewski and Pruyn 1998; Henry and Thomas 2002) and between height growth and radial growth (Larson 1965; Valinger 1992; Telewski and Pruyn 1998; Meng et al. 2006). As selection pressure resulted in trees possessing great plasticity (homeostasis) to compensate for the growth of the part experiencing the stresses, it has been suggested that the partition of resources between below- and above-ground parts is controlled by external environmental stresses (Hunt and Nickolls 1985). There have been little studies to assess the impacts of those environmental stresses, individually or interactively, on the C allocation of the plants, but also the interacting relationship of each functional part, e.g., hydraulic conduct, leaf area, and mechanical strength. The closest has been Mitchell (2003) who tested the roles of shading, mechanical stimuli and fertilization on above growth morphology of Douglas-fir seedlings grown for one summer.

Predicting growth response of trees receiving thinning treatments

One of the problems still puzzling growth and yield modelers is how to precisely predict the growth response of trees following silvicultural treatments, such as spacing, thinning and fertilization. Past models aimed to predict basal area growth of stands receiving thinning treatments primarily focused on the changes of density and competition (Sharma et al. 2002; Larocque 2002), or addition of a thinning response factor (Hawenauer et al. 1996). As stands receiving thinning treatments responded differently from the self-thinning by natural process, it remains problematic to assume that a released tree will respond to post-thinning density in the same way as a tree in an un-thinned stand would respond to current stand density. There were models designed to estimate the effects of silvicultural treatments and environmental factors on stand growth and yield based upon crown related variables (Stone 1996). However, its thinning response was only built on the basis that tree crowns grow into unoccupied space that becomes available around the tree after treatment. Critical processes such as increased wind stress after treatment are neglected. Studies have shown that increased wind exposure to a tree in the years immediately after thinning has substantial impact on C allocation on its radial and height growth (Liu et al. 2002). Therefore, a model incorporating the effects of increased wind pressure, as well as the changes of crown size on stem growth, should have a better prediction of stem growth for trees receiving thinning treatment. The new model I proposed in this study incorporating the wind effects and crown size had a good prediction of basal area growth for trees grown at a wide range of stand densities. I anticipated it will also be suitable for prediction of the growth response for trees receiving thinning treatments, but this will need to be tested.

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APPENDIX I: Derivation of pulling force (P) at the tethering point under the wind load, using the force method (Hibbeler, 1999)

To derive the pulling force caused by the wind load, the principle of superposition was applied, which states the total displacement in a structure subjected to several external loadings can be determined by adding together the displacements caused by each of the external loads acting separately (Hibbeler, 1999). This was done by choosing the pulling force as "redundant" and temporarily removing its effect on the stem so that the stem then becomes statically determinate and stable. As a result, the wind force F will cause the stem to be potentially displaced a_1 at the tethering height (Figure 3-3 A). By superposition, however, the unknown pulling force P causes the stem at the tethering height to be potentially displaced a_2, which is opposite to a_1 (Figure 3-3 B). The potential displacement of a_1 and a_2 were calculated as:

$$a_1=\frac{F}{6EI}\{3(L_1+L_2+1.3)*(L_2+1.3)^2-(L_2+1.3)^3\} \tag{3-17}$$

$$a_2=-\frac{P(L_2+1.3)^3}{3EI} \tag{3-18}$$

Where, E is modulus of elasticity; I is the moment of inertia (Hibbeler, 1999).

As the tethered trees were held firmly at the tethering height, it was assumed there was no displacement incurred at that point; therefore, the pulling force can be obtained by relating the following equation: a1+a2=0.

$$\frac{F}{6EI}\{3(L_1+L_2+1.3)*(L_2+1.3)^2-(L_2+1.3)^3\}=\frac{P(L_2+1.3)^3}{3EI} \tag{3-19}$$

$$P=0.5F(3\frac{L_1+L_2+1.3}{L_2+1.3}-1) \tag{3-20}$$

It was observed, in spite of the tight tethering, the tethered trees still had slight displacement during the gusty winds. If this displacement was set as k, then based on the principle of superposition, a1+a2=k.

$$\frac{F}{6EI}\{3(L_1+L_2+1.3)*(L_2+1.3)^2-(L_2+1.3)^3\}-\frac{P_1(L_2+1.3)^3}{3EI}=k \tag{3-21}$$

Where, k is the true displacement; P_1 is the pulling force when the displacement at the

tethering height is k.

With E being set as 7.4 GPa for lodgepole pine (Dean et al. 2002), and k being set as 20cm, it was calculated that, when F varied from 50N to 200N, the average pulling force P_1 was reduced by less then 5% comparing to P which had no displacement. Therefore, slight displacement had only minor impact on the estimation of the bending stress and bending moment.

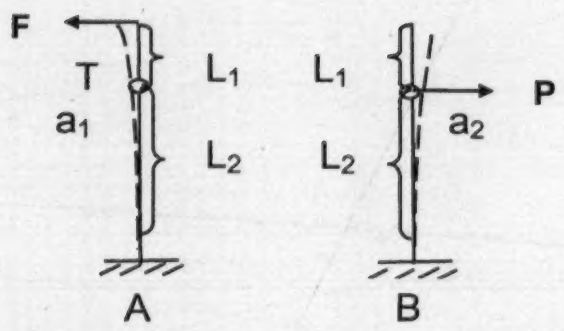

Figure 3-3. Deformed shapes of tethered stems A) under the wind load F only; B) under the pulling force P only. Where a_1 and a_2 are potential displacements at the tethering point caused by F and P respectively; T denotes the height of tethering; L_1 is the leverage from center of the crown to 10m height; L_2 is the distance from 10m height to 1.3m height.